A PROBAINOGNATHIAN CYNODONT FROM SOUTH AFRICA AND THE PHYLOGENY OF NONMAMMALIAN CYNODONTS

JAMES A. HOPSON[1] AND JAMES W. KITCHING[2]

ABSTRACT. A new small cynodont from subzone B of the *Cynognathus* Assemblage Zone (earliest Middle Triassic) of South Africa is described as *Lumkuia fuzzi*. It is represented by a nearly complete skull and lower jaw, a shoulder girdle and forelimb, and articulated dorsal and caudal vertebrae. It is placed in the eucynodont clade Probainognathia on the basis of four unequivocal synapomorphies, including absence of a parietal foramen and expanded plates on the ribs and a secondary palate extending posteriorly to the level of the orbit. *Lumkuia* is the oldest and most primitive probainognathian represented by adequate material. A cladistic analysis strongly supports the monophyly of Cynodontia, Epicynodontia (a new taxon including *Galesaurus*, *Thrinaxodon*, and eucynodonts), and Eucynodontia. The analysis also supports the eucynodont clades Probainognathia and Cynognathia, and Gomphodontia as a subgroup of the latter. Within Probainognathia, a chiniquodontid clade and a tritheledontid + mammaliaform clade are well supported. *Probainognathus* is sister to the latter clade, but this node breaks down in trees two steps longer than the shortest tree. Tritylodontids are deeply nested within the traversodont gomphodonts, with "*Scalenodon*" *hirschoni* weakly supported as their sister taxon.

INTRODUCTION

The Eucynodontia (Kemp, 1982, 1988), that is, those cynodonts more derived than the basal Triassic *Thrinaxodon*, have traditionally been divided into a carnivorous line leading to mammals and a herbivorous, or gomphodont, line leading to the Jurassic tritylodontids (Crompton and Ellenberger, 1957; Crompton, 1972b; Hopson and Kitching, 1972; Sues, 1985; Hopson and Barghusen, 1986; Hopson, 1991b, 1994). However, Kemp (1982, 1983, 1988) noted that tritylodontids and mammals share many derived features that are absent in Triassic cynodonts, which led him to suggest that tritylodontids should be separated from the herbivorous cynodonts and placed in the carnivorous line close to Mammalia; the herbivorous specializations of tritylodontids thus would be convergent on those of gomphodonts. Rowe (1986, 1988, 1993) went still further in obliterating the distinction between the carnivorous and herbivorous lineages by interleaving Middle Triassic to Early Jurassic cynodonts in a paraphyletic series of carnivorous and gomphodont taxa that lead to a terminal clade Mammaliamorpha, containing tritylodontids and traditionally defined mammals (termed Mammaliaformes by Rowe). The sister-group relationship of Tritylodontidae and Mammaliaformes has become widely accepted (Wible, 1991; Lucas and Luo, 1993; Martinez et al., 1996), although Sues (1985) and Hopson (1991b, 1994) have argued against it.

The senior author (Hopson, 1990, 1991a,b, 1994) has summarized the results of his cladistic analyses of cynodont relationships, although, to date, has not published the data on which they are based. Hopson recognizes a primarily herbivorous clade that includes tritylodontids, the Cynognathia of Hopson and Barghusen (1986), and a carnivorous clade that includes mammals, which has been designated Probainognathia (Hopson, 1990). A data matrix of synapsids as a whole was published by Sidor and Hopson (1998), but it lacks critical taxa and characters for

[1] Department of Organismal Biology and Anatomy, University of Chicago, 1027 East 57th Street, Chicago, Illinois 60637.

[2] Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa.

resolving lower-level relationships within nonmammalian cynodonts.

In May, 1988, while studying in the Karoo fossil collection of the Bernard Price Institute for Palaeontological Research (BPI) at the University of the Witwatersrand, Hopson noted a small skull and partial skeleton (BP/1/2669) from the *Cynognathus* Assemblage Zone. The specimen was identified in the catalog as a juvenile *Trirachodon*, but its skull morphology more closely resembled that of *Probainognathus* and the Chiniquodontidae, carnivorous eucynodonts best known from the Middle and Late Triassic of South America. A notice of the specimen, with preliminary conclusions on its phylogenetic significance, was presented at the 48th annual meeting of the Society of Vertebrate Paleontology (Hopson and Kitching, 1988).

This new cynodont is named and briefly described here. It is compared with *Thrinaxodon*, as a member of a more primitive cynodont grade; with *Probainognathus* and chiniquodontids, as members of the Probainognathia; and with *Cynognathus* and early gomphodont genera, as members of the Cynognathia. One purpose of this paper is to justify the establishment of the eucynodont clades Cynognathia (*sensu* Hopson and Barghusen, 1986) and Probainognathia (*sensu* Hopson, 1990, 1991a, 1994).

MATERIALS AND METHODS

Specimen BP/1/2669 had been partially prepared at the BPI so that portions of the skeleton were exposed on both sides of a small sandstone slab. The skull and lower jaws were subsequently removed from the slab and more fully prepared by Ms. Claire Vanderslice. Although portions of the external surface of the skull are damaged, the palate, braincase, and medial surface of the lower jaw are beautifully preserved. Because the postcranial elements are, for the most part, heavily eroded, they have been further prepared only slightly.

Comparisons with other cynodonts are based on specimens, stereophotographs, notes and drawings, and published accounts. The data matrix of cynodonts includes characters published by Sidor and Hopson (1998), with many new characters added, particularly from the dentition. The matrix was analyzed using the 3.1 version of PAUP (Swofford, 1993). In the following section, phylogenetic definitions of a number of suprageneric taxa are given, with a distinction made between node-based and stem-based definitions, as recommended by Sereno (1999).

SYSTEMATIC PALEONTOLOGY

Therapsida Broom, 1905

Cynodontia Owen, 1861

Definition. The most inclusive clade including Mammalia and excluding *Bauria*. This clade and its sister group, the Therocephalia (defined as the most inclusive clade including *Bauria* and excluding Mammalia), are stem-based members of a node-based Eutheriodontia (defined as the least inclusive clade including Mammalia and *Bauria*). (See Sereno [1999] for discussion of node-stem triplets.)

Epicynodontia new taxon

Definition. The most inclusive clade including Mammalia and excluding *Procynosuchus*. This clade includes, among others, *Galesaurus*, *Thrinaxodon*, and eucynodonts.

Eucynodontia Kemp, 1982

Definition. The least inclusive clade including Mammalia and *Exaeretodon*. This is a node-based taxon, with two stem-based subgroups: Cynognathia (defined as the most inclusive clade including *Exaeretodon* and excluding *Probainognathus*) and Probainognathia (defined below). Within Cynognathia is a major stem-based subgroup, the Gomphodontia (defined as the most inclusive clade including *Exaeretodon* and excluding *Cynognathus*).

Probainognathia Hopson, 1990

Definition. The most inclusive clade including *Probainognathus* and excluding *Exaeretodon.*

Family LUMKUIIDAE new family

Definition. The most inclusive clade including *Lumkuia* and excluding *Ecteninion.*

Lumkuia fuzzi new genus and species

Etymology. The generic name is from the Lumku Mission, near which the specimen was found. The species name is in honor of A. W. "Fuzz" Crompton, in recognition of his distinguished career as a student of cynodonts and early mammals.

Holotype. BP/1/2669, partial skeleton, including skull with lower jaws; left scapulocoracoid and clavicle, interclavicle, and proximal part of right clavicle; most of left forelimb; and two articulated segments of the axial skeleton; the latter consist of 10 dorsal vertebrae with associated ribs and eight caudal vertebrae.

Horizon and Locality. The specimen is from the Burgersdorp Formation, in subzone B of the *Cynognathus* Assemblage Zone. It was collected by Father Paul Reubsamen in the vicinity of the Lumku Catholic Mission, near the town of Lady Frere, Eastern Cape Province, South Africa.

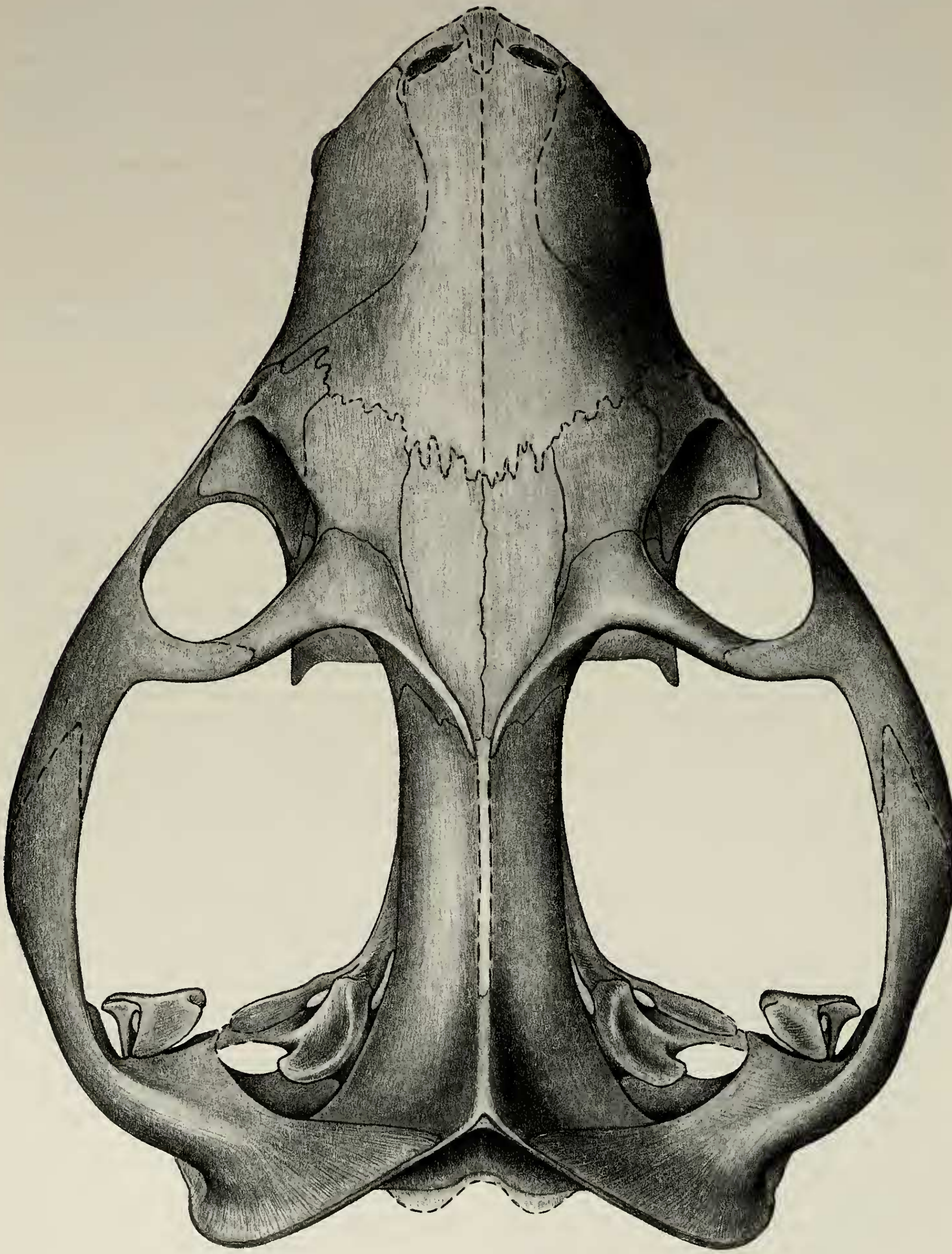
Age. The *Cynognathus* Assemblage Zone in the region of Lady Frere is represented by subzone B of Hancox et al. (1995; B. S. Rubidge, personal communication), which is considered to be of early Middle Triassic (Anisian) age (Hancox and Rubidge, 1997).

Diagnosis. Lumkuia fuzzi is characterized by a unique combination of primitive and derived features. It possesses the following probainognathian features: parietal foramen absent; rear of secondary palate lies below anterior border of orbit; expanded plates on ribs absent. It is more primitive than other probainognathians in that the frontal extends down the medial orbital wall only to the level of the lacrimal foramina and an orbital process of the palatine is lacking. It is more primitive than other eucynodonts in that the dentary does not extend as far posteriorly, resulting in a longer dorsal exposure of the surangular between the rear of the dentary and the articular. At the rear of primary palate is an autapomorphic feature: the pterygoids form a deep median depression with a nearly vertical posterior wall, behind which they form a prominent median boss anterior to the interpterygoidal vacuities. The presence of interpterygoidal vacuities suggests that the type specimen may be a subadult individual.

DESCRIPTION

Skull

In dorsal view (Fig. 1), the general appearance of the skull of *Lumkuia* is similar to that of *Thrinaxodon,* although the preorbital region is shorter and the temporal fossa longer. Thus, the center of the orbits lies anterior to the middle of the skull, whereas in *Thrinaxodon* the orbits are centered exactly at midlength. The pterygoid flanges, which in *Thrinaxodon* lie below the middle of the orbits, are visible in *Lumkuia* behind the postorbital bar (as they commonly are in eucynodonts). As in *Thrinaxodon,* the sagittal crest terminates above the occiput, so that the occipital condyles are visible from above. This contrasts with *Ecteninion* and *Probainognathus* (although not chiniquodontids), in which the sagittal crest overhangs the occiput and covers the condyles. The lambdoidal crests in *Lumkuia,* as in *Thrinaxodon,* diverge at greater than 90 degrees and extend posteriorly at their outer ends only a short distance beyond the occipital condyles. In *Probelesodon* and *Chiniquodon,* and in gomphodonts, the sagittal crest terminates slightly in front of the condyles but the lambdoidal crests diverge at an acute angle and extend back well beyond the condyles. The zygomatic arches of *Lumkuia* are more flared and rounded in pro-



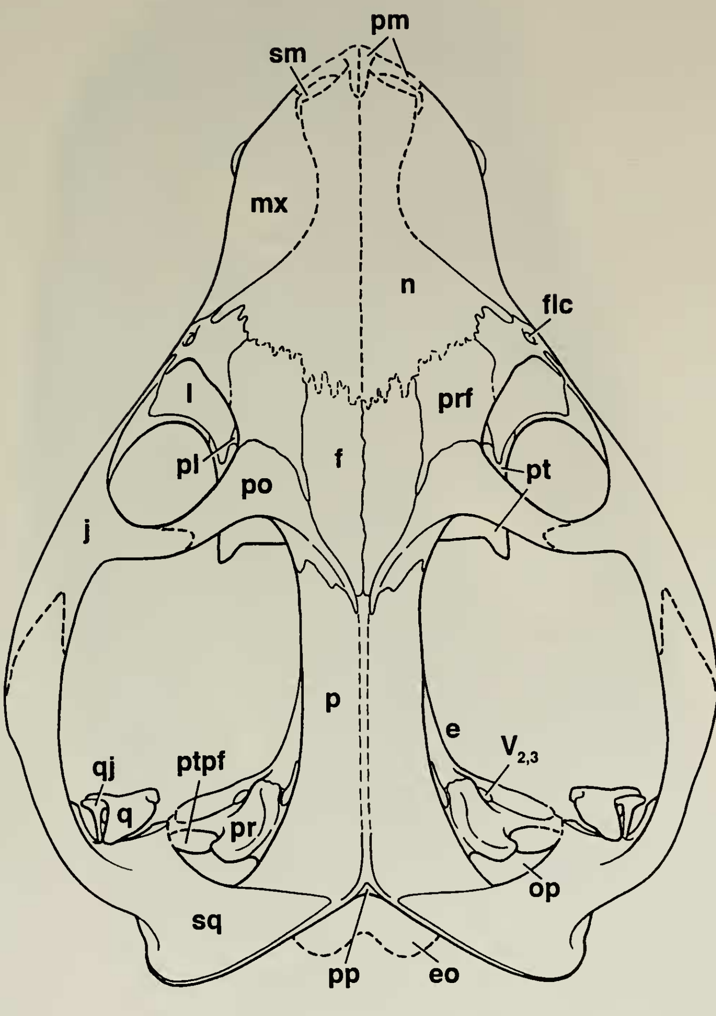
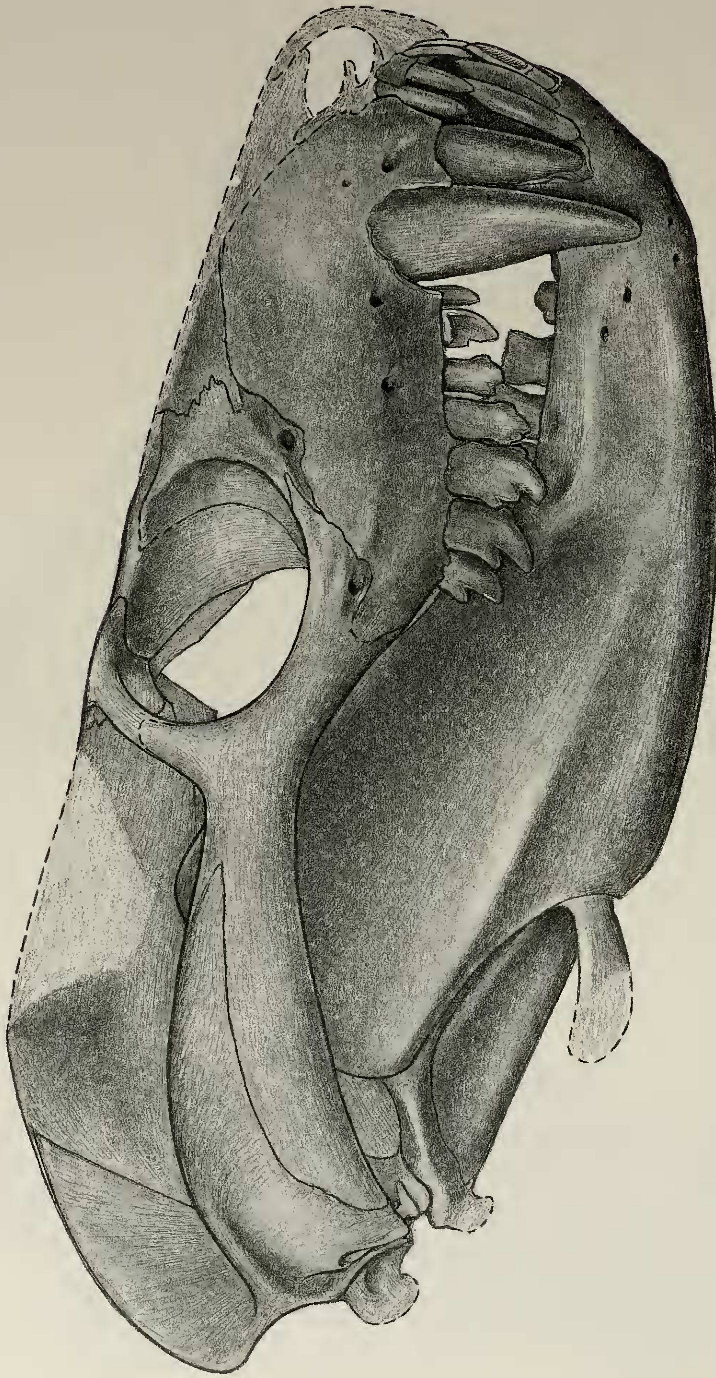


Figure 1. Skull of *Lumkuia fuzzi* (BP/1/2669) in dorsal view (on left enlarged ×3). Scale bar = 10 mm. Abbreviations: e, epipterygoid; eo, exoccipital; f, frontal; flc, foramen of lacrimal canal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pp, postparietal; pr, prootic; prf, prefrontal; pt, pterygoid; ptpf, pterygoparoccipital foramen; q, quadrate; qj, quadratojugal; sm, septomaxilla; sq, squamosal; $V_{2,3}$, trigeminal foramen.



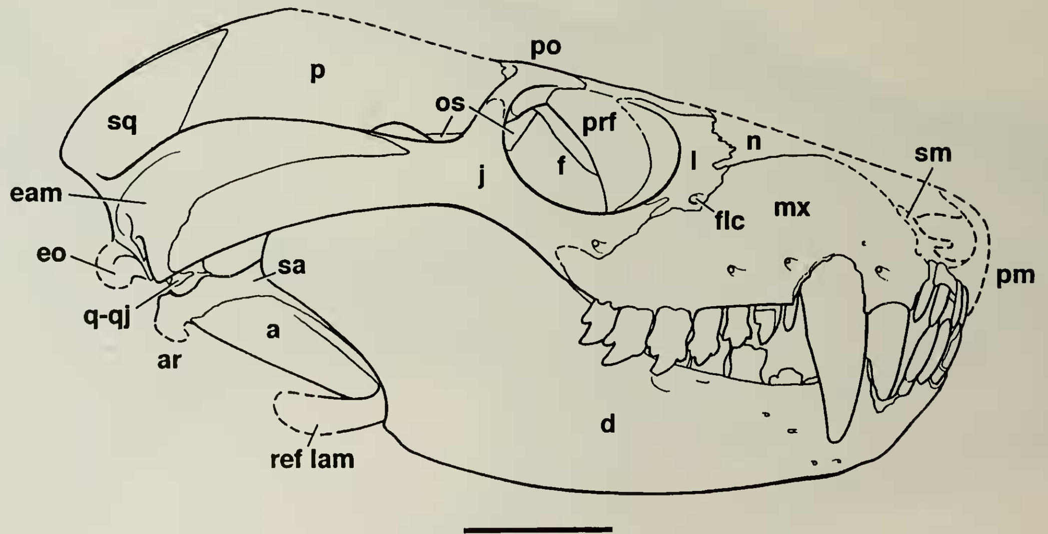
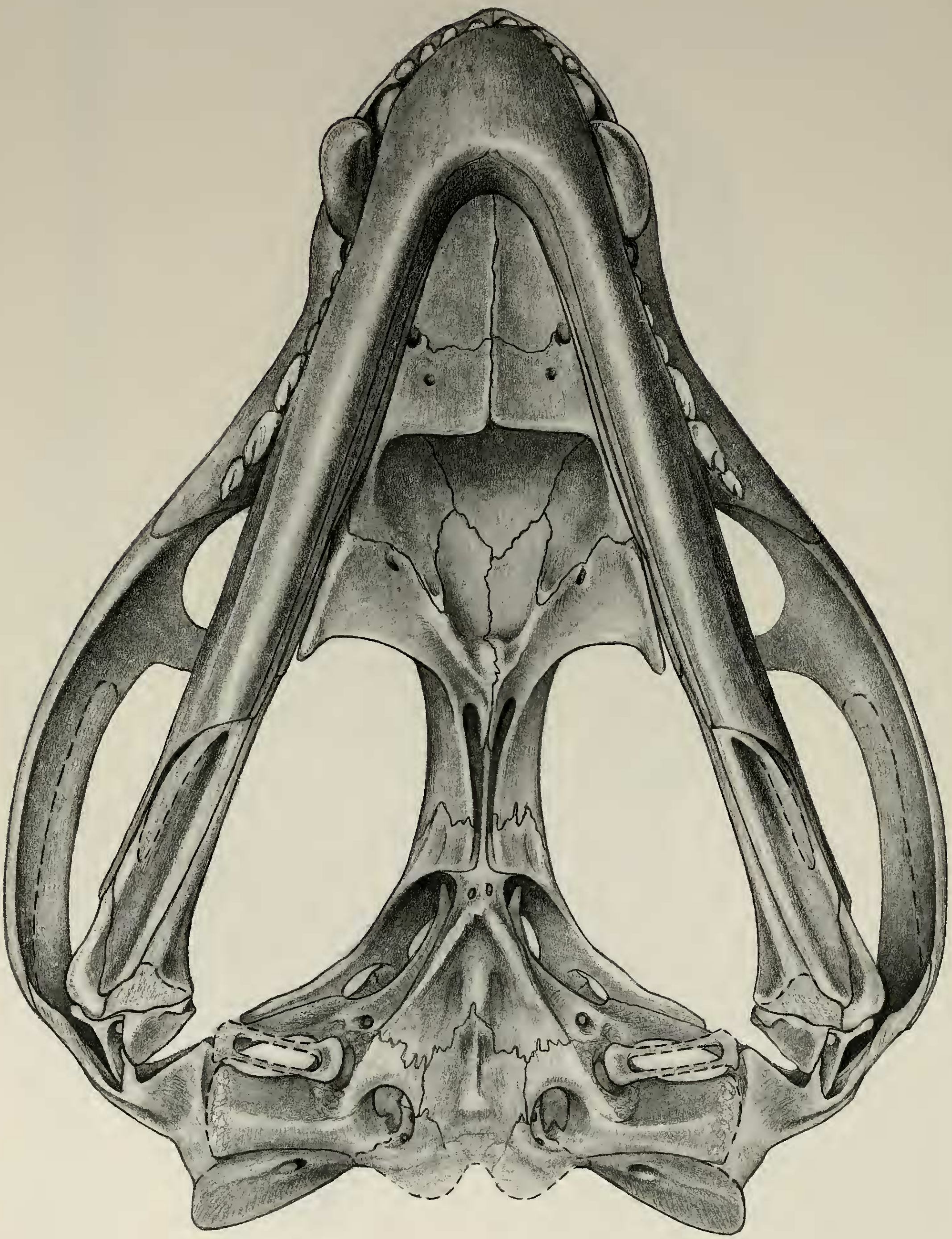


Figure 2. Skull of *Lumkuia fuzzi* (BP/1/2669) in lateral view (on left enlarged ×3). Scale bar = 10 mm. Abbreviations: a, angular; ar, articular; d, dentary; eam, external auditory meatus; eo, exoccipital; f, frontal; flc, foramen of lacrimal canal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; os, orbitosphenoid; p, parietal; pm, premaxilla; po, postorbital; prf, prefrontal; q-qj, quadrate–quadratojugal; ref lam, reflected lamina; sa, surangular; sm, septomaxilla; sq, squamosal.



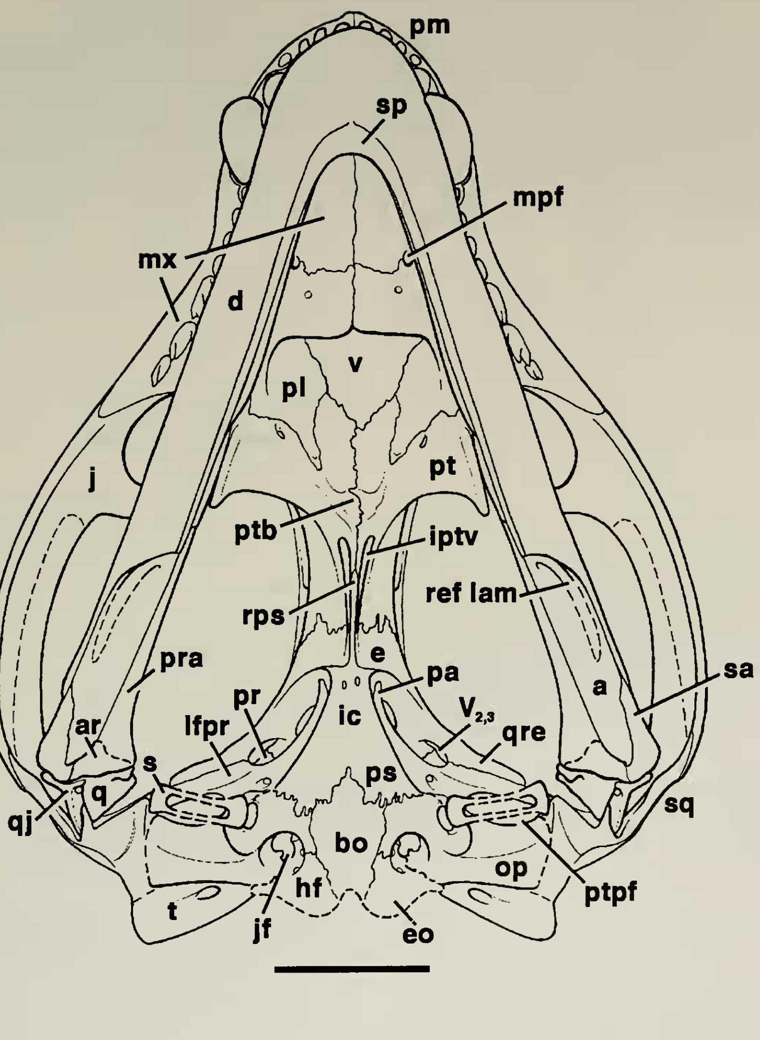


Figure 3. Skull of *Lumkuia fuzzi* (BP/1/2669) in ventral view (on left enlarged ×3). Scale bar = 10 mm. Abbreviations: a, angular; ar, articular; bo, basioccipital; d, dentary; e, epipterygoid; eo, exoccipital; hf, hypoglossal foramina; ic, internal carotid foramina; iptv, interpterygoidal vacuity; j, jugal; jf, jugular foramen; lfpr, lateral flange of prootic; mpf, major palatine foramen; mx, maxilla; op, opisthotic; pa, pila antotica; pl, palatine; pm, premaxilla; pr, prootic; pra, prearticular; ps, parasphenoid; pt, pterygoid; ptb, pterygoid boss; ptpf, pterygoparoccipital foramen; q, quadrate; qj, quadratojugal; qre, quadrate ramus of epipterygoid; ref lam, reflected lamina; rps, parasphenoid rostrum; s, stapes; sa, surangular; sp, splenial; sq, squamosal; t, tabular; v, vomer.

file than those of *Thrinaxodon,* being widest anterior to, rather than at, the level of the jaw joint; in this *Lumkuia* resembles other Triassic probainognathians and differs from cynognathians.

In lateral view (Fig. 2), the skull and lower jaw of *Lumkuia* appear to be more robust than in *Thrinaxodon* (Fig. 5A), due to the shorter snout, longer temporal region, and deeper dentary. Also, as in other eucynodonts except *Cynognathus* (Fig. 6A), the jaw joint is located more anteriorly, so that the lambdoidal crests extend well behind the articular region. The canines are more robust and the posterior cheek teeth proportionately larger than in *Thrinaxodon* and *Probainognathus* (Fig. 5C), although not in *Ecteninion* and chiniquodontids. The zygomatic arch appears to be no more robust than that of *Thrinaxodon,* except perhaps posteriorly, whereas that of *Probainognathus,* and especially of chiniquodontids and cynognathians, is much deeper.

In ventral view (Fig. 3), the symphyseal region is shorter than that of *Thrinaxodon* and the shorter jaws diverge at a greater angle. The secondary palate is only slightly more developed, with a nearly straight rather than concave posterior margin. Behind the pterygoid flanges, the basicranial axis is more transversely compressed than in *Thrinaxodon,* so that the subtemporal fossa is proportionately wider.

In occipital view (Fig. 4), the most distinctive difference from *Thrinaxodon* is in the constriction of the base of the zygomatic arch and the separation of the zygoma from the more flaring lambdoidal crest by a V-shaped notch. In noneucynodonts, such as *Procynosuchus, Galesaurus,* and *Thrinaxodon,* the lambdoidal crest is continuous with the dorsal ridge on the zygomatic arch. Only in eucynodonts, with the exception of *Cynognathus,* is there a distinct break between the two crests, with the lambdoidal crest passing back posterior to the medial end of the dorsal zygomatic ridge.

The individual skull bones are briefly described below, with only salient features noted. The facial portions of the premaxilla and septomaxilla are missing. On the palate, backwardly pointing processes of the premaxillae separate the elongate, slitlike, incisive foramina. The premaxilla forms all but the posteriormost parts of the lateral border of the incisive foramen and the fossa for the lower canine.

The alveolar border of the maxilla is straight, turning up slightly at the level of the last tooth and passing smoothly into the suborbital bar where, a short distance behind the last postcanine, it contacts the jugal. In the palate, the maxilla contributes to the rear margin of the incisive foramen and the posteriormost part of the lower canine fossa. The maxilla forms the anterior two thirds of the secondary palate, extending as far back as the gap between the third and fourth postcanines. The major palatine foramen opens anteroventrally on the maxillary–palatine suture well lateral to the midline.

The nasals have largely flaked off, leaving some bone only posterolaterally. As shown by impressions on the surface of the frontals, the nasals overlap the frontals and the nasofrontal suture lies a short distance behind the anterior border of the orbit.

The eroded dorsal surface of the frontals preserves a slightly undulating midline suture. The contact with the parietals on the skull roof is not preserved, but probably lay between the posteriormost part of the temporal crests of the postorbitals. In the medial wall of the orbit, a thin strip of frontal is exposed behind the large descending flange of prefrontal, extending ventrally about to the level of the lacrimal foramina.

Within the orbit, the prefrontal overlies the frontal and is itself overlain by the lacrimal; it extends ventrally nearly to the level of the palatine on the dorsal surface of the palate.

The lacrimal has a short exposure on the face compared with that of *Thrinaxodon* or *Probainognathus.* Within the orbit, it

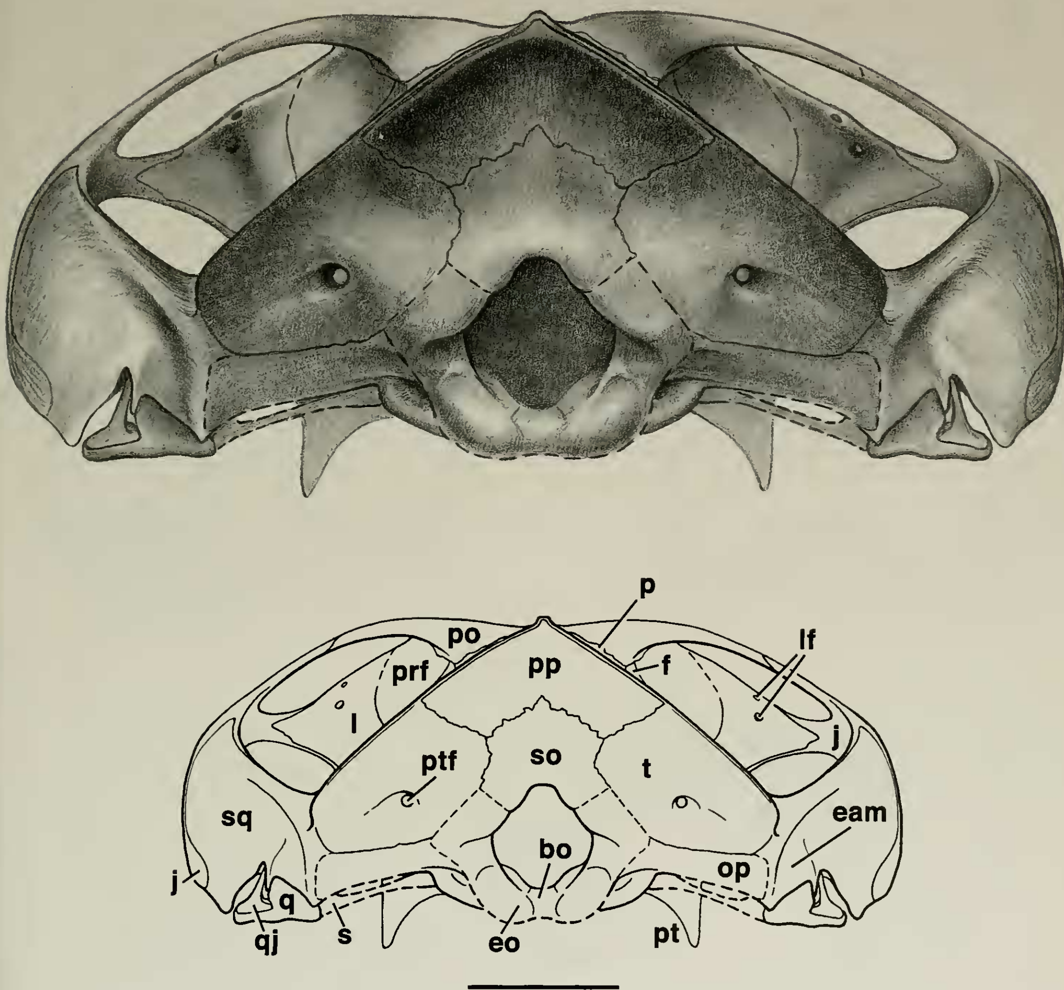


Figure 4. Skull of *Lumkuia fuzzi* (BP/1/2669) in occipital view (upper drawing enlarged ×3). Scale bar = 10 mm. Abbreviations: bo, basioccipital; eam, external auditory meatus; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; lf, lacrimal foramina; op, opisthotic; p, parietal; po, postorbital; pp, postparietal; prf, prefrontal; pt, pterygoid; ptf, posttemporal foramen; q, quadrate; qj, quadratojugal; s, stapes; so, supraoccipital; sq, squamosal; t, tabular.

forms the anterior half of the orbital wall and most of its floor. Paired lacrimal foramina open forward inside the anterior rim of the orbit; a small foramen opens anterolaterally from the lower lacrimal canal on to the facial portion of the lacrimal.

A posterolaterally directed process of the postorbital forms the dorsal part of the postorbital bar; it extends down internal to the postorbital process of the jugal for an indeterminate distance. The upper, more horizontal, part of the postorbital bar is roughly triangular in cross section; its posterior face forms a flat vertical surface that is continuous posteromedially with a vertical lappet of postorbital that overlies the lateral surface of the parietal. The posterior parts of the paired postorbitals converge backwards as temporal crests and merge into the median sagittal crest on the parietals. These vertical surfaces on the postorbital mark the area of attachment of

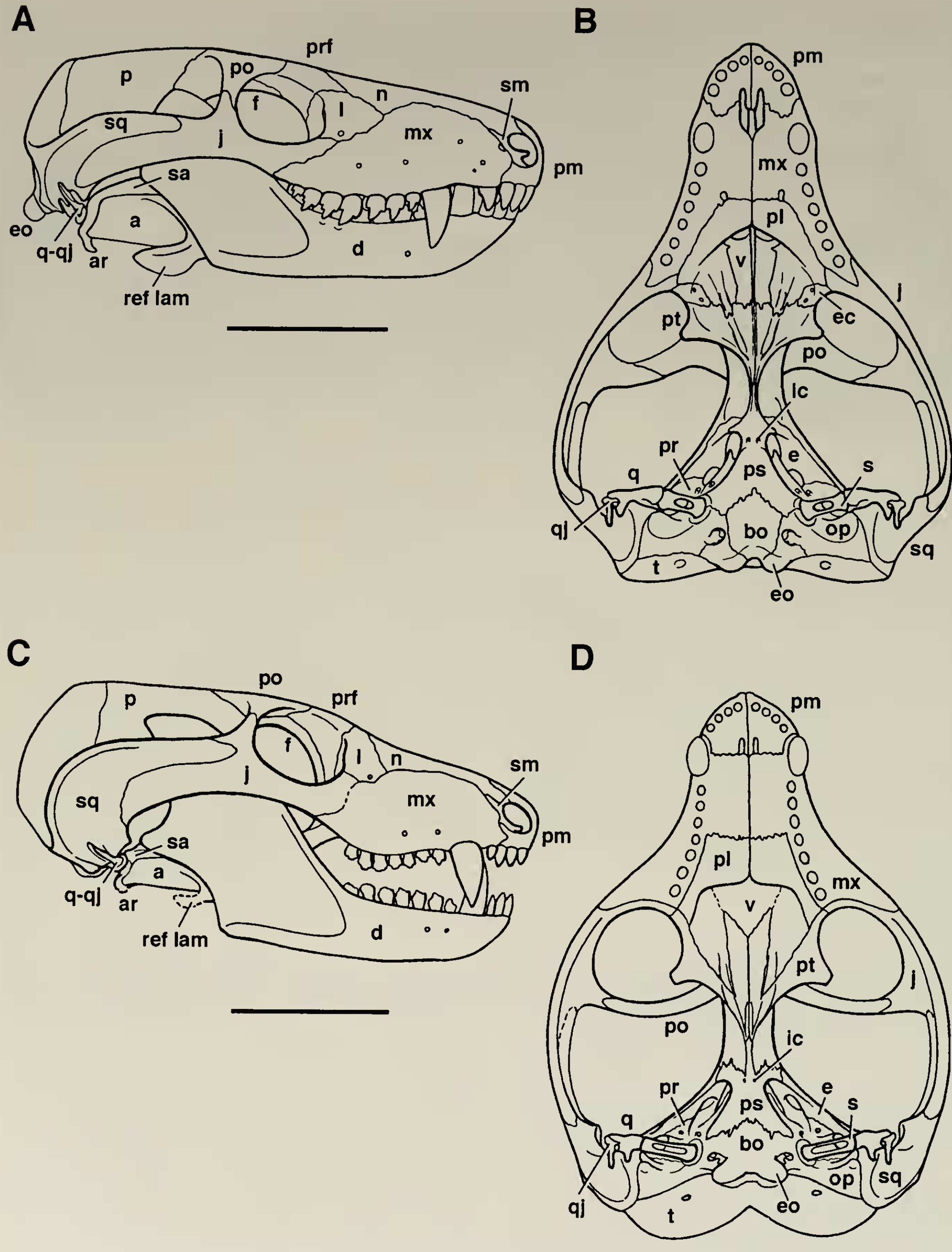


Figure 5. Skulls in lateral and ventral views of (A, B) *Thrinaxodon liorhinus*, and (C, D) *Probainognathus jenseni*. Scale bars = 20 mm. Abbreviations: a, angular; ar, articular; bo, basioccipital; d, dentary; e, epipterygoid; ec, ectopterygoid; eo, exoccipital; f, frontal; ic, internal carotid foramen; j, jugal; l, lacrimal; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pr, prootic; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; ref lam, reflected lamina; s, stapes; sa, surangular; sm, septomaxilla; sq, squamosal; t, tabular; v, vomer.

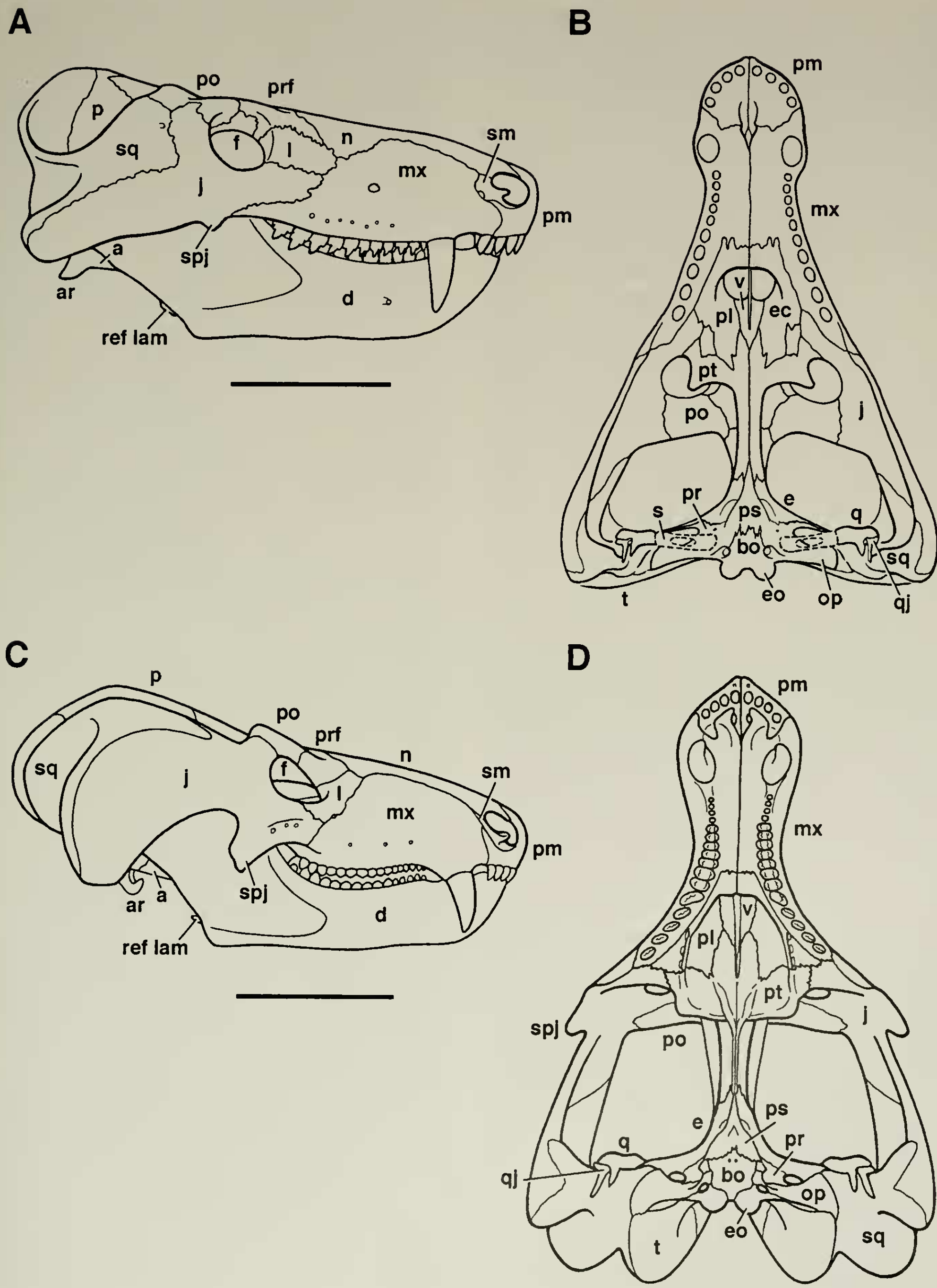


Figure 6. Skulls in lateral and ventral views of (A, B) *Cynognathus crateronotus,* and (C, D) *Diademodon mastacus.* Scale bar in A = 100 mm, in B = 90 mm. Abbreviations: a, angular; ar, articular; bo, basioccipital; d, dentary; e, epipterygoid; ec, ectopterygoid; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pr, prootic; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; ref lam, reflected lamina; s, stapes; sm, septomaxilla; spj, suborbital process of jugal; sq, squamosal; t, tabular; v, vomer.

the anteriormost portion of the temporalis muscle. A medially extending horizontal lappet of postorbital contacts the sliver of frontal exposed in the orbital wall.

The dorsal parts of the fused parietals are damaged, but enough is preserved to indicate that the sagittal crest was relatively low anteriorly and increased only moderately in height posteriorly. No evidence of a parietal foramen is preserved and it was almost certainly absent. The ventral margin of the parietal contacts the dorsal edge of the orbitosphenoid, behind which it is overlapped by the dorsal margin of the epipterygoid back to its midlength. Between the parietal and the dorsal margins of the epipterygoid and prootic is an elongate opening into the cranial cavity. Leading to this opening from behind, along the prootic–parietal suture, is a deeply incised groove that begins at the anterior opening of the posttemporal foramen. The groove presumably contained the supraorbital ramus of the ramus superior of the stapedial artery, with a meningeal branch entering the cranial cavity through the elongate opening (Rougier et al., 1992; Wible and Hopson, 1995). The parietals broaden posteriorly, where they are overlain by the cranial process of the squamosal, and contribute to the roof of the posttemporal foramen.

The jugal is a relatively slender bone, not unlike that of *Thrinaxodon* and *Probainognathus*. In the zygomatic arch, the jugal is overlain dorsally by the zygomatic process of the squamosal and bounded behind by a descending lappet of squamosal. A moderate-sized, anterolaterally directed foramen pierces the jugal below the orbit. A short distance behind the last postcanine, the jugal passes medial to the rear of the maxilla to contact the anterolateral margin of the pterygoid, and perhaps the palatine, at the anterior border of the subtemporal fossa. The jugal is exposed behind the lacrimal in the posterior part of the orbital floor.

The squamosal may be described as consisting of two portions, the cranial and zygomatic processes, separated at the level of the V-shaped notch. The cranial process is a relatively flat, triangular plate extending nearly to the apex of the posterior end of the sagittal crest. The cranial process overhangs the anterior opening of the posttemporal foramen and its flaring rear border forms the lambdoidal crest. The V-shaped notch has an anteroposteriorly rounded dorsal surface that separates the lambdoidal ridge from the dorsal ridge on the zygomatic process. Directly below the notch is a triangular lappet of squamosal that on its medial surface bears a depression for the incompletely ossified distal end of the paroccipital process. Anteromedially, the lappet appears to contact the lateral flange of the prootic. Laterally, it forms the medial wall of the recess for the quadrate, which is open behind as an inverted V-shaped emargination. The emargination is bounded laterally by a slender, pointed process that descends between the upper ends of the quadrate and quadratojugal. Further laterally, the zygomatic portion of the squamosal forms a descending process behind the jugal that in life presumably contacted the surangular (although here a contact is absent because the lower jaw appears to have shifted slightly forward). The zygomatic process curves forward from this level extending over the jugal nearly to the level of the postorbital bar. A shallow sulcus, the external auditory meatus, extends up and forward from the distal end of the paroccipital process on to the posterolateral surface of the zygoma.

The fused vomers form the center of the arched roof of the primary palate above the secondary palate and roof the choanal trough to a point just behind the level of the last postcanine.

The palatal plates of the palatines form the posterior third of the short secondary palate, underlying the posterior margins of the maxillae. A small foramen pierces the palatine a short distance posterointernal to the major palatine foramen. The rear margin of the secondary palate is thickened and slightly rugose. As in other Triassic probainognathians, the lateral margin of the secondary palate curves dorsally, so that the palatine meets the maxilla in the floor of a narrow longitudinal trough internal to the posterior postcanines. This trough continues back beyond the level of the secondary palate, where it is bounded medially by slender ridges that extend back nearly to the lateral margins of the pterygoid flanges. An ectopterygoid is not present, so the posterolateralmost part of the palatine contacts the pterygoid, and perhaps the jugal, internal to the last postcanine. The palatine is here pierced by several small foramina, with a larger opening between its posterior margin and the overlying pterygoid. The palatines form the lateral walls of the choanal trough, contacting the vomer and pterygoids medially and contributing to the anterior half of the more medial palatal ridges that bound the posterior half of the trough. The palatine is exposed on the upper surface of the primary palate as a broad plate that lacks a dorsal orbital process.

The ectopterygoid is absent. Although described in other Triassic probainognathians (Romer, 1969, 1970; Martinez et al., 1996), we believe its presence has not been convincingly demonstrated.

The pterygoids form the rear of the choanal trough, which is uniquely deep and is bordered behind by a near-vertical wall. At the posterior end of the medial palatal ridges, where they converge at the rear of the choanal trough, is a prominent median boss; this feature appears to be unique among cynodonts. Lateral to the anterior end of the medial palatal ridge, adjacent to the suture with the palatine, are one or more slitlike openings that pierce the pterygoid. Laterally, the deep, triangular pterygoid flanges descend well down the inside of the lower jaws. The ridges forming their rear margins converge posteriorly and extend on to the basipterygoid rami of the pterygoids, nearly meeting where the latter contact the basipterygoid processes of the basisphenoid. An elongate gap between the ridges is divided by the long rostrum of the parasphenoid to form paired interpterygoidal vacuities. Such vacuities are present in *Dvinia* and *Procynosuchus* and in juveniles of *Thrinaxodon* (Estes, 1961), but are usually absent in postprocynosuchid cynodonts.

The orbitosphenoid is roughly the shape of an elongate half-cylinder, with a U-shaped cross section. It lies on the midline below the postorbitals and parietals in the space between the postorbital bar and the anterodorsal end of the epipterygoid.

The ascending lamina of the epipterygoid is extremely long fore to aft, being nearly twice the length of the prootic portion of the braincase sidewall. This contrasts sharply with the condition in *Probainognathus* and *Ecteninion,* in which the ascending lamina tapers anterodorsally and is much shorter than the prootic. The ascending lamina is suturally joined to the anterodorsal margin of the prootic above the anterior border of the large trigeminal foramen. The epipterygoid contacts the basicranial wing of the pterygoid ventrally and appears to have a short medial contact with the basipterygoid process. Its quadrate ramus is a shallow vertical lamina that extends back below the trigeminal foramen to meet the lateral flange of the prootic. The epipterygoid continues back for a short distance in contact with the lateral flange, terminating at the level of the anterior border of the pterygoparoccipital foramen. That portion of the epipterygoid behind the basipterygoid joint forms the lateral wall of a ventrally open space, the cavum epiptericum.

The basisphenoid consists of slightly expanded anterior basipterygoid processes that contact the pterygoids and epipterygoids, a very narrow middle portion that underlies the sella turcica and is pierced by paired carotid foramina, and an expanded posterior part that contacts the prootic dorsally and the basioccipital posteriorly. The dermal parasphenoid is fused to its ventral surface, forming a near-horizontal, triangular plate posteriorly that covers the basisphenoid–basiooccipital contact. Further forward, the parasphenoid passes between the carotid foramina and forms an elongate midline process, the rostrum, that extends forward between the pterygoids to separate the interpterygoidal vacuities. The anterior end of the parasphenoid is suturally joined to the pterygoids immediately behind and dorsal to the median pterygoid boss.

The prootic portion of the ossified otic capsule lacks a sutural separation from the opisthotic portion, although the prootic typically contributes to the anterior part of the paroccipital process and rim of the fenestra ovalis. The lateral flange of the prootic extends posterolaterally from behind the trigeminal foramen; although the distal end of the lateral flange is damaged, it undoubtedly contacted the squamosal in life, thus enclosing the large, oval, pterygoparoccipital foramen. The lateral surface of the prootic bears a slight groove that extends between the latter opening and the trigeminal foramen. Such a groove is usual in cynodonts, although here it is unusually faint. The system of grooves and foramina in the lateral surface of the prootic are interpreted as transmitting arteries and veins (see Rougier et al., 1992; Wible and Hopson, 1995). Deep to the outer margin of the trigeminal foramen, the ossified pila antotica extends anterodorsally approximately to the level of the basipterygoid joint. Just in front of the fenestra ovalis is the small, posterolaterally directed foramen for the facial (VIIth) nerve.

The opisthotic forms the posterior half of the rim of the fenestra ovalis; most of the paroccipital process; and the anterior, anteromedial, and lateral borders of the jugular foramen. The ventral surface of the paroccipital process slopes up and forward from its rounded posteroventral margin, to form the posterodorsal wall of the middle ear cavity (Hopson, 1966). The opisthotic contacts the basioccipital medially and the exoccipital posteromedially and posterolaterally on the margins of the jugular foramen. This foramen is confluent within the opisthotic with the space occupied by the inner ear. Deep within the jugular foramen is a low ridge that extends a short distance into the opening from its posterolateral wall. This ridge in more derived cynodonts, such as *Probainognathus* (Fig. 5D) and *Massetognathus* (Rougier et al., 1992, figs. 7B, D), is a long fingerlike projection that extends toward the medial wall of the foramen. In tritheledontids, tritylodontids, and mammaliaforms, the foramen is fully subdivided, with a true jugular foramen posteriorly (transmitting nerves and vessels from the cranial cavity), and a perilymphatic foramen anteriorly (transmitting the perilymphatic duct from the inner ear cavity).

The basioccipital is exposed midventrally behind the parasphenoid, with which it has an interdigitating transverse suture. It forms the midventral part of the foramen magnum, bearing a narrow transverse articular facet for the atlas intercentrum.

The paired exoccipitals form the occipital condyles, damaged here, which extend about one third of the distance up the lateral sides of the foramen magnum. More dorsally, they meet the supraoccipital, but the sutural contact cannot be distinguished. The exoccipital contributes to the posteromedial wall of the jugular foramen, which bears a shallow depression in which lie two hypoglossal foramina, a smaller anterior one and a larger posterior one, which open into the cranial cavity shortly in front of the occipital condyle.

The median supraoccipital forms an indeterminate part of the dorsal border of the foramen magnum. The supraoccipital is overlain by the tabular laterally and the postparietal above. The postparietal occupies the upper surface of the occiput above the supraoccipital and tabulars and between the flaring lambdoidal crests. Middorsally, the postparietal has a short, pointed process that extends forward between the fused parietals. The tabulars occupy the entire occiput lateral to the supraoccipital, completely surrounding the small, circular posttemporal foramina.

The quadrate is exposed on the right side, where it has shifted slightly forward from its contact with the squamosal. The transversely oriented articular condyle of the quadrate is about as wide as the total bone is high. The flat posterior surface of its ascending process is oriented obiquely to the transverse axis and fits against a matching surface on the anterior face of the squamosal. The posterolateral third or so of the quadrate is exposed from behind in the inverted V-shaped emargination of the squamosal. The lateral end of the quadrate condyle extends well beyond the outer margin of the ascending process; its dorsal surface is clasped by the transversely expanded lower end of the quadratojugal.

The quadratojugal has a transversely compressed ascending process that fits into a narrow groove in the squamosal behind the lateral part of the ascending process of the quadrate. The quadratojugal is separated from the quadrate posteriorly by a thin descending prong of squamosal. The lower end of the bone is expanded transversely, its medial portion overlying the lateral condyle of the quadrate and its lateral portion forming a free rounded process.

An incomplete right stapes is preserved nearly in situ, its oval footplate separated slightly from the depression that houses the fenestra ovalis. The preserved posterior crus of the stapes extends anterolaterally toward the medial surface of the quadrate condyle.

Lower Jaw

The right lower jaw is essentially complete and well preserved. The large dentary consists of a deep tooth-bearing horizontal ramus and a broad ascending process (for insertion of jaw-closing muscles), each forming about one half of its length. The short, deep symphysis is fused. The anteroventral surface of the fused dentaries bears numerous tiny foramina. Two small mental foramina lie below the first and second postcanines. At the posterior end of the convex lower margin of the dentary is a slightly projecting pseudangular process, above which the lower margin of the bone curves up and back over the postdentary elements. A low outturned ridge overlies the surangular and angular and continues forward across the masseteric fossa, fading into its surface below the last upper postcanine. The masseteric fossa extends forward as a slight depression to the level of the fifth upper postcanine. The coronoid process rises slightly above the dorsal border of the zygomatic arch just behind the postorbital bar. The lateral surface of the coronoid process forms a broad, slightly concave trough between out-turned anterodorsal and posteroventral borders. The slightly convex posterior margin of the process slopes down to meet the surangular about 5 mm anterior to the articular glenoid.

As is usual in eucynodonts, the laterally exposed postdentary bones are much shallower than in *Thrinaxodon* (Fig. 5A), with their lower border sloping up and back. The surangular has less exposure behind the dentary than in *Thrinaxodon,* but more than in other eucynodonts, where the dentary nearly reaches the articular (Figs. 5C, 6A, C). On the medial surface of the jaw, the surangular has a flat dorsal surface that is buttressed by an overlying ridge on the dentary. The exposed part of the surangular behind the dentary has a transversely thickened upper margin. Anterolateral to the articular glenoid is a slightly raised area that in life may have contacted the descending flange of the squamosal; however, it lacks the prominent articular boss that contacts the squamosal in *Cynognathus* and *Diademodon* (Crompton, 1972a).

The angular covers most of the surangular laterally and has a dorsal ridge that overhangs its concave outer surface. The reflected lamina is damaged, but it appears to be more slender than that of *Thrinaxodon.* The articular is transversely narrower than in *Thrinaxodon,* more closely resembling that of *Probainognathus* and *Probelesodon.* The remaining postdentary elements are similar to those of *Thrinax-*

odon, except that the splenials are fused in the rear of the symphysis.

Dentition

The dental formula is: I4/3, C1/1, Pc7/5. The incisors are all small and closely spaced. The canines are long and broad, with extremely robust roots. The canines have a rounded anterior surface and, in the uppers at least, an unserrated ridge posteriorly.

The upper postcanines increase in size from first to sixth, with the seventh being slightly smaller than the fifth. The first three have a slightly recurved main cusp and a small posterior accessory cusp. The fourth is well preserved on the left, where it possesses a large recurved main cusp, a smaller accessory cusp behind it, and a second, much smaller, posterior accessory cusp near the base of the crown. Anterior, and slightly internal, to the main cusp is a very small accessory cusp; this cusp is absent on the right, perhaps obliterated by wear. Upper postcanine 5 is much larger than Pc^4, but is nearly identical in morphology. Upper postcanine 6 has a small anterointernal cusp, a strongly recurved main cusp, and a smaller recurved posterior accessory cusp. The rear of the crown is damaged, so the presence of a second posterior cusp is uncertain. The damaged seventh postcanine has a recurved main cusp followed by an accessory cusp, but the presence of additional cusps is uncertain. The teeth are set at a slight angle to the line of the tooth row, so that, where present, the posterior accessory cusp contacts the succeeding crown lingual to its anterior accessory cusp.

The lower postcanines are less fully exposed. The first tooth is damaged, but the well-preserved second closely resembles the fourth upper postcanine; both resemble a typical lower postcanine of *Thrinaxodon.* The crowns of Pc_{3-5} are exposed lingually; the third and fourth have an anterior accessory cusp and at least one posterior accessory cusp, whereas the fifth has two posterior accessory cusps, although the presence of an anterior accessory cusp cannot be determined. Both upper and lower postcanines appear to lack lingual cingula.

Postcranial Skeleton

The poorly preserved shoulder girdle, forelimb, and caudal vertebrae show no unusual features and will not be described. The dorsal vertebral series, although not well preserved, merits description inasmuch as it possesses features that distinguish probainognathians from cynognathians. The articulated section of the dorsal vertebral column contains 10 vertebrae exposed in ventral view. On the partially exposed left side, the last two vertebrae show a pair of articulating zygapophyses, thus establishing directionality along the column. The last nine vertebrae preserve ribs. Of these, the last two possess features that together characterize cynodont lumbar vertebrae (Jenkins, 1971): the rib attachments are entirely on the vertebral body, and these ribs are synostosed to the vertebrae with a serrate suture. In the more anterior ribs, the capitular articulation spans two adjacent centra; whether any are synostosed is uncertain, although the first rib, at least, appears to be free.

The anterior four pairs of ribs are damaged distally, but they appear to be anteroposteriorly compressed, thus resembling typical thoracic ribs. The posterior five sets of ribs appear to be short, because their more or less rounded ends retain some matrix distally. These ribs are perhaps slightly broader than those preceding them, but they do not expand distally to any noticeable degree. The last rib is broader than the preceding ones, as is the last (second) lumbar vertebra of *Cynognathus* illustrated by Jenkins (1971, fig. 15A). Also as in *Cynognathus,* the last three sets of ribs curve slightly forward. However, at a comparable distance from the proximal synostosis, the posterior ribs of *Lumkuia* show no trace of the distal expansions seen in *Galesaurus, Thrinaxodon, Cynognathus,* and *Diademodon* (Jenkins, 1971). Thus, they resemble the lumbar ribs of the probainognathians *Probelesodon* and *Probainognathus* (Romer, 1973).

PHYLOGENETIC RELATIONSHIPS OF *LUMKUIA FUZZI*

A cladistic analysis of cynodonts was performed, with 23 cynodont taxa and the basal therocephalian *Lycosuchus* and a gorgonopsid as successive outgroups (see Appendix 2). Of 101 characters, 43 are from the skull, 9 from the lower jaw, 29 from the dentition, and 20 from the postcranial skeleton (see Appendix 1). The aims of most past phylogenetic analyses have been to order therapsid taxa with respect to mammals, hence only taxa and characters that served to do this were included. We have made a special effort to include a large sample of gomphodont taxa and to include characters, particularly from the postcanine dentition, that would specifically aid in resolving their interrelationships. The data were analyzed using a random addition sequence with 10 replicates and the tree bisection–reconnection (TBR) algorithm of PAUP 3.1 (Swofford, 1993), with the resulting character distribution optimized under delayed transformation (DELTRAN).

Although resolution of the phylogenetic relationships of tritylodontids with respect to tritheledontids and mammaliaforms is not the principal aim of this study, we have attempted to determine where these three taxa are placed under different treatments of the characters. When all characters were run unordered, the tritheledontid *Pachygenelus* and the mammaliaform *Morganucodon* were the sister group of Tritylodontidae, nested deeply within the gomphodont clade (tree length = 233; Consistency Index (CI) = 0.58; Retention Index (RI) = 0.78; Rescaled CI = 0.45). When a minimum of four multistate characters (18, 22, 63, 73) were ordered, *Pachygenelus* and *Morganucodon* shifted to a probainognathian clade, where they remained under tests of cladogram robustness (see below). This is the cladogram illustrated here (Fig. 7).

The analysis (with four ordered characters) resulted in three most parsimonious trees of 238 steps (CI = 0.57; RI = 0.77; RC = 0.44). The trees differ only in the placement of the basal cynodonts *Dvinia* and *Procynosuchus* with respect to "higher" cynodonts, either in a trichotomy with the latter, as their sister clade, or with *Procynosuchus* and *Dvinia* as their successive outgroups. The cladogram (Fig. 7) shows the last (our preferred) alternative.

Three near-basal clades are supported by large numbers of unequivocal synapomorphies: Cynodontia by 26, Epicynodontia by 14, and Eucynodontia by 11. A dichotomy within Eucynodontia includes a well-characterized Cynognathia, with eight unequivocal synapomorphies, and a less well-characterized Probainognathia, with four unequivocal (and two equivocal) synapomorphies. Within Cynognathia, the Gomphodontia are characterized by five unequivocal (and two equivocal) synapomorphies. Within the latter clade, the paraphyletic traversodonts (including Tritylodontidae as a derived subgroup) are characterized by three unequivocal (and one equivocal) synapomorphies. Characters diagnosing each clade are listed in Appendix 3.

Lumkuia is the basal member of the Probainognathia, although *Ecteninion* from the early Late Triassic is more derived in but a single feature: a frontal–palatine contact in the orbital wall. *Probelesodon, Chiniquodon,* and *Aleodon* represent a monophyletic Chiniquodontidae, characterized by a very long secondary palate and a posterior angulation of the maxilla. *Probainognathus* is allied with the tritheledontid/mammaliaform clade by two synapomorphies: the presence of postcanine lingual cingula and a medial shift of the maxillary tooth rows. *Pachygenelus* and *Morganucodon* form an extremely robust clade, supported by 18 unequivocal synapomorphies. Although this clade shares many character states with tritylodontids, the latter are deeply nested within the Gomphodontia on the basis of numerous cynognathian and gomphodont synapomorphies.

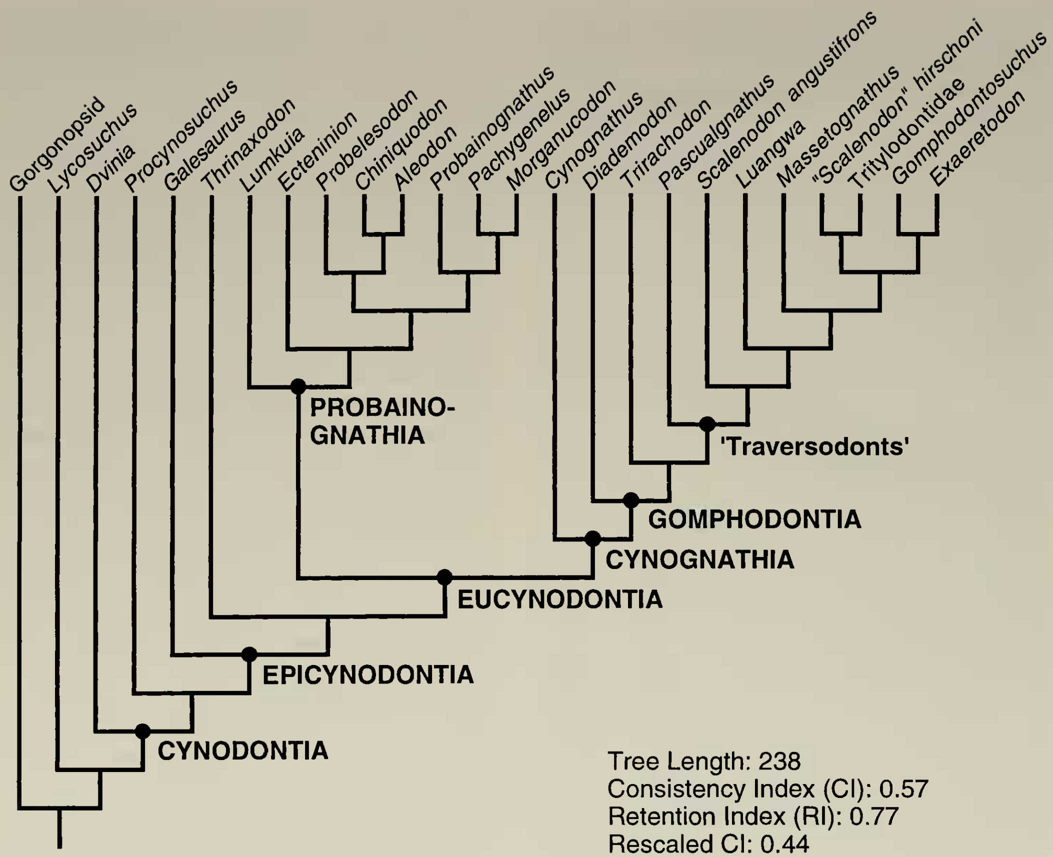


Figure 7. Cladogram of nonmammalian cynodonts. One of three shortest trees (238 steps in length), in which *Dvinia* is sister taxon to remaining cynodonts. "Traversodonts" refers to *Pascualgnathus* and more derived gomphodonts, usually designated as Traversodontidae. However, inclusion of Tritylodontidae in this "family" makes it paraphyletic, hence use of the informal term "traversodonts."

The robustness of this cladogram was tested by generating trees of incrementally greater length (up to six steps longer) to determine where specific nodes break down. At one step longer (239 steps), in the strict consensus of 59 trees, nearly all resolution within Eucynodontia breaks down, leaving only the grouping of the chiniquodontids *Aleodon* + *Chiniquodon* and of *Pachygenelus* + *Morganucodon*. However, the 50% majority-rule consensus tree has the same topology as the minimum-length tree. At two steps longer, in the 50% majority-rule consensus of 286 trees, the node between *Probainognathus* and *Ecteninion* breaks down, yielding a trichotomy with a chiniquodontid + *Pachygenelus/Morganucodon* clade. At three steps longer, in the 50% majority-rule consensus of 1,024 trees, the node between Tritylodontidae and "*Scalenodon*" *hirschoni* breaks down. At four steps longer (3,480 trees), the node between *Probelesodon* and the remaining chiniquodontids breaks down. Only in the 50% majority-rule consensus of 30,120 trees that are six steps longer than the minimum-length tree does the node between *Lumkuia* and the remaining probainognathians break down (Fig. 8). A probainognathian clade occurs in 75% of these trees and cynognathian and gomphodont clades both oc-

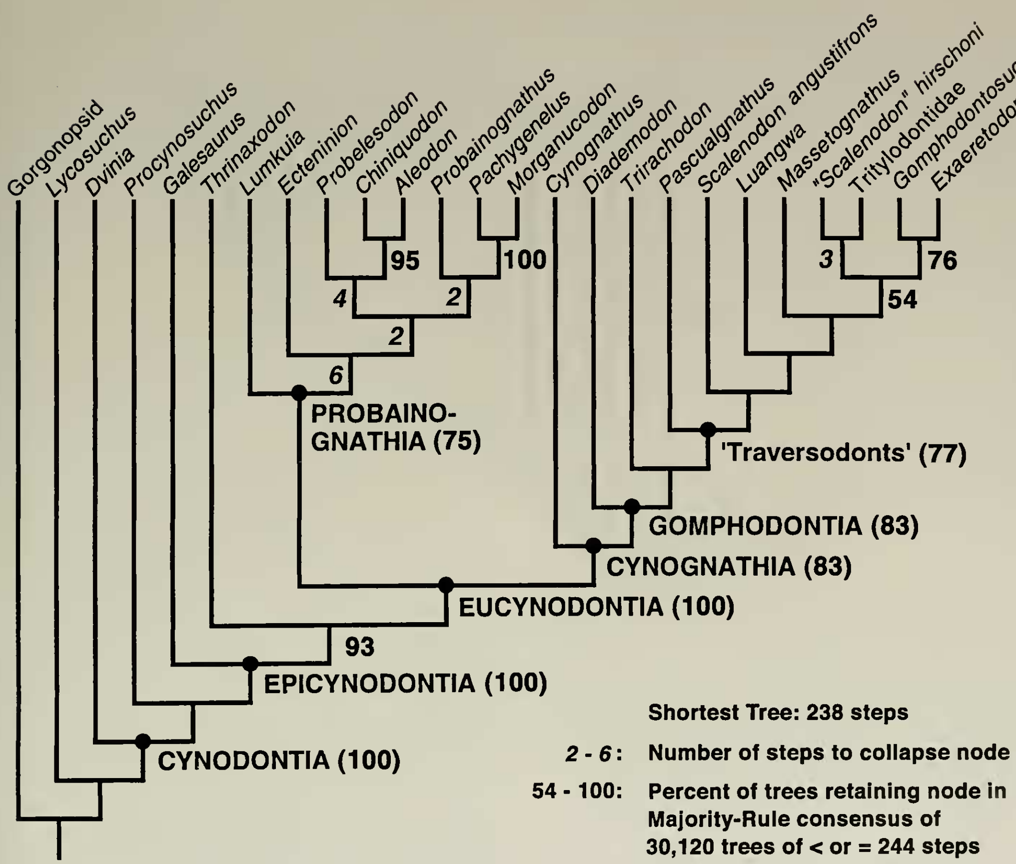


Figure 8. Cladogram of nonmammalian cynodonts. Shortest tree (238 steps) is shown, with numbers in bold italics (***2–6***) indicating the number of steps required to collapse that node, and numbers in bold (**54–100**) indicating the percentage of trees retaining that node in a 50% majority-rule consensus of 30,120 trees of less than or equal to 244 steps (six steps longer than minimum-length tree).

cur in 83% of the trees. The gomphodont genera retain the ordering seen in the minimum length tree in the great majority of trees that are six steps longer. Tritylodontids and "S." *hirschoni* form a trichotomy with the *Exaeretodon/Gomphodontosuchus* clade in 54% of these trees.

In order to determine how parsimonious our preferred tree is to that of Rowe (1993, fig. 10.2), we used MacClade (Maddison and Maddison, 1992) to order our 19 eucynodont taxa in the most parsimonious tree in which the cynognathian–probainognathian dichotomy is not recognized. This turned out to duplicate the order of the far fewer taxa in Rowe's cladogram except that tritheledontids, not tritylodontids, form a clade with mammaliaforms (Fig. 9A). This tree is 267 steps long, 29 steps longer than our preferred tree. In the comparison of this tree with our preferred tree (Fig. 9B), the distribution of the internal carotid foramina is shown. Absence of these foramina in the basisphenoid is a synapomorphy of Cynognathia (Fig. 9B). When the cynognathian–probainognathian dichotomy is eliminated, the distribution of this character becomes extremely unparsimonious, with the foramina lost, regained, then lost and subsequently regained again.

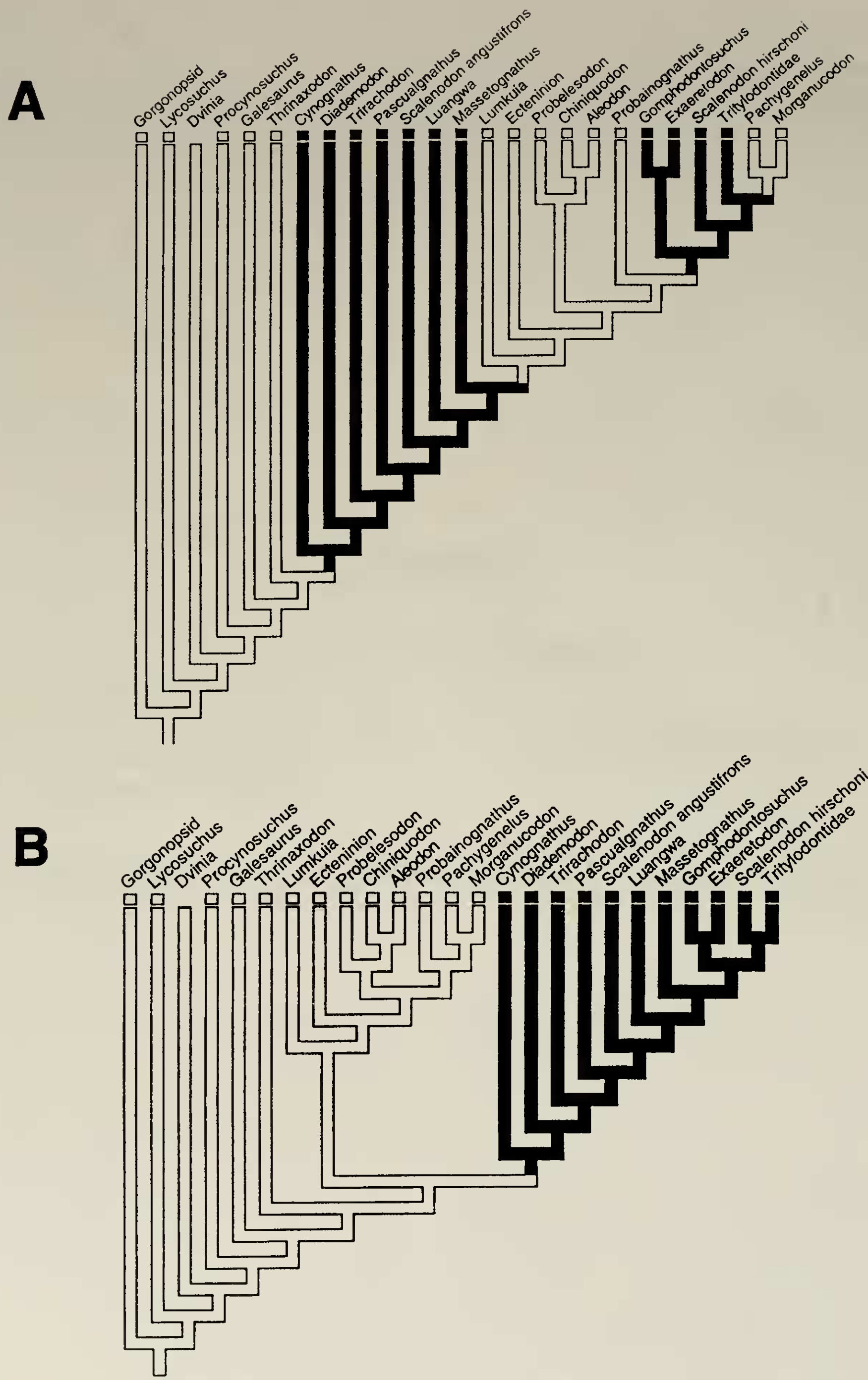


Figure 9. Cladograms constructed using MacClade showing distribution of internal carotid foramina in basisphenoid (character 26). Absence of carotid foramina is derived (black). (A) Cladogram in which 19 eucynodont taxa are ordered in the most

CONCLUSIONS

Lumkuia fuzzi is a basal member of the eucynodont clade Probainognathia. The dichotomy of eucynodonts into Probainognathia and Cynognathia is supported by this analysis, as is the placement of the Tritylodontidae within the cynognathian subgroup Gomphodontia. The sister group relationship of Tritheledontidae and Mammaliaformes is extremely well supported, although their placement in Probainognathia, rather than as sister to tritylodontids within Cynognathia, is less firm, requiring the ordering of four characters to achieve this placement. This uncertainty results from the extraordinarily large number of derived (mammallike) features shared by these three groups, features treated in other recent analyses as synapomorphies but here shown more likely to be convergences. A definitive solution to this phylogenetic problem will be found when morphologic intermediates between typical Triassic cynodonts and these primarily Jurassic (and, in the case of mammaliaforms, later) taxa are incorporated into analyses. Within the gomphodonts, *Exaeretodon* has a very mammallike postcranial skeleton and helps bridge the morphologic gap between Middle Triassic gomphodonts and tritylodontids. Bonaparte and Barberena (2001) describe two Late Triassic carnivorous cynodonts that are also very mammallike postcranially, and that appear to bridge the gap between *Probainognathus* and tritheledontids/mammaliaforms in cranial and dental morphology. We believe these newly described Late Triassic cynodonts will provide critical evidence supporting the probainognathian–cynognathian dichotomy and the occurrence of a truly extraordinary amount of homoplasy in eucynodont evolution.

ACKNOWLEDGMENTS

We thank Drs. M. A. Raath and B. S. Rubidge for the loan of material; Ms. Claire Vanderslice for preparation and illustration of specimens; and Mr. C. A. Sidor and Drs. G. W. Rougier, J. R. Wible, and J. A. Wilson for help in preparation of the manuscript. Hopson's research was supported by National Science Foundation grants BSR 86-15016 and 89-06619. We are grateful to Dr. F. A. Jenkins, Jr., and his co-organizers of the symposium for providing this opportunity to honor Fuzz Crompton. Hopson also wishes to express his pleasure at attending the symposium and enjoying the fellowship of good friends and colleagues.

LITERATURE CITED

BONAPARTE, J. F., AND M. C. BARBERENA. 2001. On two advanced carnivorous cynodonts from the Late Triassic of Southern Brazil. Bulletin of the Museum of Comparative Zoology, **156:** 59–80.

BROOM, R. 1905. On the use of the term Anomodontia. Records of the Albany Museum, **1:** 266–269.

CROMPTON, A. W. 1972a. The evolution of the jaw articulation of cynodonts, pp. 231–253. *In* K. A. Joysey and T. S. Kemp (eds.), Studies in Vertebrate Evolution. Edinburgh: Oliver and Boyd. 284 pp.

———. 1972b. Postcanine occlusion in cynodonts and tritylodontids. Bulletin of the British Museum (Natural History) Geology, **21:** 29–71.

CROMPTON, A. W., AND F. ELLENBERGER. 1957. On a new cynodont from the Molteno Beds and the origin of the tritylodontids. Annals of the South African Museum, **44:** 1–14.

ESTES, R. 1961. Cranial anatomy of *Thrinaxodon liorhinus.* Bulletin of the Museum of Comparative Zoology, Harvard, **125:** 165–180.

HANCOX, P. J., AND B. S. RUBIDGE. 1997. The role of fossils in interpreting the development of the Karoo Basin. Palaeontologia Africana, **33:** 41–54.

HANCOX, P. J., M. A. SHISHKIN, B. S. RUBIDGE, AND J. W. KITCHING. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical

←

parsimonious tree that does not recognize a probainognathian–cynognathian dichotomy. Tree length is 267 steps, 29 steps longer than tree shown in (B), in which eucynodont taxa are ordered in the most parsimonious tree, determined from PAUP analysis (see Fig. 8). In this tree, the node-based Eucynodontia comprises the stem-based Probainognathia and Cynognathia. Absence of carotid foramina is a synapomorphy of Cynognathia. In tree A, CI = 0.51, RI = 0.71, RC = 0.36. In tree B, CI = 0.57, RI = 0.77, RC = 0.44.

implications. South African Journal of Science, **91:** 143–144.

HOPSON, J. A. 1966. The origin of the mammalian middle ear. American Zoologist, **6:** 437–450.

———. 1990. Cladistic analysis of therapsid relationships. Journal of Vertebrate Paleontology, **10**(3, Suppl.): 28A.

———. 1991a. Convergence in mammals, tritheledonts, and tritylodonts. Journal of Vertebrate Paleontology, **11**(3, Suppl.): 36A.

———. 1991b. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synapsids, pp. 635–693. *In* H.-P. Schultze and L. Trueb (eds.), Origins of the Higher Groups of Tetrapods: Controversy and Consensus. Ithaca, New York: Comstock Publishing Associates, a Division of Cornell University Press. xii + 724 pp.

———. 1994. Synapsid evolution and the radiation of non-therian mammals, pp. 190–219. *In* D. R. Prothero and R. M. Schoch (eds.), Major Features of Vertebrate Evolution, Short Courses in Paleontology, No. 7. Knoxville: University of Tennessee. 270 pp.

HOPSON, J. A., AND H. R. BARGHUSEN. 1986. An analysis of therapsid relationships, pp. 83–106. *In* N. Hotton III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), The Ecology and Biology of Mammal-Like Reptiles. Washington, D.C.: Smithsonian Institution Press. x + 326 pp.

HOPSON, J. A., AND J. W. KITCHING. 1972. A revised classification of cynodonts. Palaeontologia Africana, **14:** 71–85.

———. 1988. A *Chiniquodon*-like cynodont from the Early Triassic of South Africa and the phylogeny of advanced cynodonts. Journal of Vertebrate Paleontology, **8**(3, Suppl.): 18A.

JENKINS, F. A., JR. 1971. The postcranial skeleton of African cynodonts. Bulletin of the Peabody Museum, Yale University, **36:** 1–216.

KEMP, T. S. 1982. Mammal-Like Reptiles and the Origin of Mammals. London: Academic Press. xiv + 363 pp.

———. 1983. The relationships of mammals. Zoological Journal of the Linnean Society, **77:** 353–384.

———. 1988. Interrelationships of the Synapsida, pp. 1–22. *In* M. J. Benton (ed.), The Phylogeny of the Tetrapods, Vol. 2: Mammals, Systematics Association Special Volume 35B. Oxford: Clarendon Press. 323 pp.

LUCAS, S. G., AND Z. LUO. 1993. *Adelobasileus* from the Upper Triassic of West Texas: the oldest mammal. Journal of Vertebrate Paleontology, **13:** 309–334.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade, Version 3.01. Sunderland, MA: computer program distributed by Sinauer Associates, Inc.

MARTINEZ, R. N., C. L. MAY, AND C. A. FORSTER. 1996. A new carnivorous cynodont from the Ischigualasto Formation (Late Triassic, Argentina), with comments on eucynodont phylogeny. Journal of Vertebrate Paleontology, **16:** 271–284.

OWEN, R. 1861. Palaeontology, or a Systematic Summary of Extinct Animals and Their Geological Relations, second edition. Edinburgh: Adam and Black. xvi + 463 pp.

ROMER, A. S. 1969. The Chañares (Argentina) Triassic reptile fauna. V. A new chiniquodontid cynodont, *Probelesodon lewisi*—cynodont ancestry. Breviora, **333:** 1–24.

———. 1970. The Chañares (Argentina) Triassic reptile fauna. VI. A chiniquodontid cynodont with an incipient squamosal–dentary jaw articulation. Breviora, **344:** 1–18.

———. 1973. The Chañares (Argentina) Triassic reptile fauna. XIX. Postcranial materials of the cynodonts *Probelesodon* and *Probainognathus*. Breviora, **407:** 1–26.

ROUGIER, G. W., J. R. WIBLE, AND J. A. HOPSON. 1992. Reconstruction of the cranial vessels the early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial vascular system. Journal of Vertebrate Paleontology, **12:** 188–216.

ROWE, T. 1986. Osteological diagnosis of Mammalia, L. 1758, and its relationship to extinct Synapsida. Ph.D. dissertation. Berkeley: University of California. 446 pp.

———. 1988. Definition, diagnosis, and origin of Mammalia. Journal of Vertebrate Paleontology, **8:** 241–264.

———. 1993. Early mammal phylogenetic systematics, pp. 129–145. *In* F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials. New York: Springer-Verlag. x + 249 pp.

SERENO, P. C. 1999. Definitions in phylogenetic taxonomy: critique and rationale. Systematic Biology, **48:** 329–351.

SIDOR, C. A., AND J. A. HOPSON. 1998. Ghost lineages and "mammalness": assessing the temporal pattern of character acquisition in the Synapsida. Paleobiology, **24:** 254–273.

SUES, H.-D. 1985. The relationships of the Tritylodontidae (Synapsida). Zoological Journal of the Linnean Society, **85:** 205–217.

SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Champaign, Illinois: computer software and documentation distributed by Illinois Natural History Survey.

WIBLE, J. R. 1991. Origin of Mammalia: the craniodental evidence reexamined. Journal of Vertebrate Paleontology, **11:** 1–28.

WIBLE, J. R., AND J. A. HOPSON. 1995. Homologies of the prootic canal in mammals and non-mammalian cynodonts. Journal of Vertebrate Paleontology, **15:** 331–356.

APPENDIX 1: CHARACTER LIST

States are denoted as (0) = primitive state; (1), (2), and (3) = derived states.

Cranium

1. Premaxilla forms posterior border incisive foramen: absent (0), present (1).
2. Nasal–lacrimal contact: absent (0), present (1).
3. Prefrontal: present (0), absent (1).
4. Postfrontal: present (0), absent (1).
5. Postorbital: present (0), absent (1).
6. Prefrontal–postorbital contact: absent (0), present (1).
7. Parietal foramen: present (0), absent (1).
8. Vomer internarial shape: broad plate (0), parallel-sided keel (1).
9. Ectopterygoid: contacts maxilla (0), does not contact maxilla (1), absent (2).
10. Interpterygoid vacuity in adult between pterygoid flanges: present (0), absent (1).
11. Palatal exposure of maxilla behind canine greater than 20% distance from canine to posterior end of palatine: absent (0), present (1).
12. Secondary palatal plate on maxilla: absent (0), present, does not reach midline (1), present, reaches midline (2).
13. Secondary palatal plate on palatine: absent or low ridge (0), present, extends nearly to midline (1), present, reaches midline (2).
14. Length secondary palate relative to toothrow: shorter (0), about equal (1), longer (2).
15. Length secondary palate relative to anterior border of orbit: shorter (0), about equal (1), longer (2).
16. Teeth on pterygoid flange: present (0), absent (1).
17. Ventral surface of basisphenoid depressed below occipital condyles: less than ¼ occipital height (0), greater than ¼ occipital height (1).
18. Zygomatic arch dorsoventral height: slender (0), moderately deep (1), very deep (2).
19. Zygomatic arch dorsal extent: below middle of orbit (0), above middle of orbit (1).
20. Jugal depth in zygomatic arch relative to exposed squamosal depth: less than twice (0), greater than twice (1).
21. Jugal suborbital process: absent (0), present (1).
22. Squamosal groove for external auditory meatus: shallow (0), moderately deep (1), very deep (2).
23. Frontal–palatine contact in orbit: absent (0), present (1).
24. Tabular extends around posttemporal foramen: absent (0), present (1).
25. Descending flange of squamosal lateral to quadratojugal: absent (0), present not contacting surangular (1), present contacting surangular (2).
26. Internal carotid foramina in basisphenoid: present (0), absent (1).
27. Groove on prootic extending from pterygoparoccipital foramen to trigeminal foramen: absent (0), present and open (1), present and enclosed as a canal (2).
28. Trigeminal nerve exit: between prootic incisure and epipterygoid (0), via foramen between prootic and epipterygoid (1), via two foramina (2).
29. Quadrate contact: primarily squamosal (0), primarily crista parotica (1).
30. Quadrate ramus of pterygoid: present (0), absent (1).
31. Quadrate posteroventral process in squamosal posterior notch: absent (0), present (1).
32. Epipterygoid ascending process at level of trigeminal foramen: rodlike (0), moderately expanded (1), greatly expanded (2).
33. Epipterygoid–prootic overlap: absent (0), present (1).
34. Lateral flange of prootic: absent (0), present (1).

35. Epipterygoid–frontal contact: absent (0), present (1).
36. Separate foramina for vestibular and cochlear nerves: absent (0), present (1).
37. Double occipital condyles: absent (0), present (1).
38. Stapedial foramen orientation: anteroposterior (0), dorsoventral (1).
39. Greatest width of zygomatic arches: near middle of arch (0), at posterior end of arch (1).
40. Length of palatine relative to maxilla in secondary palate: shorter (0), about equal (1), longer (2).
41. Posterolateral end of maxilla: passes obliquely posterodorsally into suborbital bar (0), forms right angle ventral to jugal contact (1).
42. Fenestra rotunda separation from jugular foramen: confluent (0), partially separated by fingerlike projection from posterolateral wall of jugular foramen (1), completely separated (2).
43. V-shaped notch separating lambdoidal crest from zygomatic arch: absent (0), present (1).

Lower Jaw

44. Dentary symphysis: not fused (0), fused (1).
45. Dentary masseteric fossa: absent (0), high on coronoid region (1), extends to lower border of dentary (2).
46. Dentary overlap of dorsal surface of surangular: short (0). long (1).
47. Dentary coronoid process height: below middle of orbit (0), above middle of orbit (1).
48. Position of dentary–surangular dorsal contact relative to postorbital bar and jaw joint: closer to postorbital bar (0), midway between (1), closer to jaw joint (2).
49. Postdentary rod height relative to exposed length (distance between base of reflected lamina and jaw joint): greater than ½ length (0), about ½ length (1), less than ½ length (2).
50. Coronoid mediolaterally thickening: absent (0), present (1).
51. Reflected lamina of angular posterior extent relative to distance from angle of dentary to jaw joint: greater than ½ the distance (0), less than ½ the distance (1).
52. Reflected lamina of angular shape: deep corrugated plate (0), spoon-shaped plate (1), hook with depth greater than ½ length (2), hook with depth less than ½ length (3).

Dentition

53. Upper incisor number: five or more (0), four (1), three (2).
54. Lower incisor number: four or more (0), three (1), two (2).
55. Incisor cutting margins: serrated (0), smoothly ridged (1), denticulated (2).
56. Incisor size: all small (0), some or all enlarged (1).
57. Upper canine size: large (0), reduced in size (1), absent (2).
58. Lower canine size: large (0), reduced in size (1), absent (2).
59. Canine serrations: present (0), absent (1).
60. Postcanine shape: single point (0), two or more cusps in line (1).
61. Upper postcanine buccal cingulum: absent (0), present (1).
62. Postcanine lingual cingulum: absent (0), narrow (1), lingually expanded (2).
63. Number of upper cusps in transverse row: one (0), two (1), three or more (2).
64. Position of upper transverse cusp row on crown: on anterior half of crown (0), midcrown almost to posterior margin (1), at posterior margin (no posterior cingulum) (2).
65. Central cusp of upper transverse row: absent (0), midway between buccal and lingual cusps (1), closer to lingual cusp (2).
66. Longitudinal shear surface of main upper cusp: anterior and posterior

(to transverse ridge) (0), posterior only (1), anterior only (2).

67. Upper anterobuccal accessory cusp: present (0), absent (1).
68. Upper posterobuccal accessory cusp: present (0), absent (1).
69. Upper anterolingual accessory cusp: absent (0), present (1).
70. Upper anterior transverse (cingulum) ridge: low (0), high (1).
71. Upper lingual ridge: absent (0), present (1).
72. Transverse axis of crown strongly oblique to midline axis: absent (0), present (1).
73. Number of lower cusps in transverse row: one (0), two (1), three or more (2).
74. Lower anterior cingulum or cusp: absent (0), present (1).
75. Lower posterior basin: absent (0), present (1).
76. Widest lower cusp in transverse row: lingual (0), buccal (1).
77. Posterior portion maxillary tooth row inset from lateral margin of maxilla (cheek developed): absent (0), present (1).
78. Axis of posterior part of maxillary tooth row: directed lateral to subtemporal fossa (0), directed toward center of fossa (1), directed toward medial rim of fossa (2).
79. Posterior portion of maxillary tooth row extends medial to temporal fossa: absent (0), present (1).
80. Posteriormost postcanine(s) gomphodont: absent (0), present (1).
81. Postcanine replacement pattern in adult: "alternating" (0), widely spaced waves (three or more teeth/wave) (1), single wave (2).

Postcranium

82. Expanded costal plates on ribs: absent (0), present (1).
83. Lumbar costal plates with ridge overlapping preceding rib: absent (0), present (1).
84. Scapula infraspinous fossa with outturned anterior and posterior borders: absent (0), present (1).
85. Acromion process: absent (0), present (1).
86. Scapular constriction below acromion: absent (0), present (1).
87. Scapular elongation between acromion and glenoid: absent (0), present (1).
88. Procoracoid in glenoid: present (0), barely present or absent (1).
89. Procoracoid contact with scapula: greater than coracoid contact (0), equal to or less than coracoid contact (1).
90. Humerus ectepicondylar foramen: present (0), absent (1).
91. Ulna olecranon process: absent (unossified) (0), present (1).
92. Manual digit III phalanx number: four (0), three (1).
93. Manual digit IV phalanx number: five (0), four (1), three (2).
94. Length of anterior process of ilium anterior to acetabulum (relative to diameter of acetabulum): less than 1.0 (0), 1.0–1.5 (1), greater than 1.5 (2).
95. Length of posterior process of ilium posterior to acetabulum: (relative to diameter of acetabulum): between 0.5 and 1.0 (0), greater than 1.0 (1), less than 0.5 (2).
96. Dorsal profile of ilium: strongly convex (0), flat to concave (1).
97. Total length of pubis relative to acetabulum diameter: greater than 1.5 (0), between 1.5 and 1.0 (1), less than 1.0 (2).
98. Greater trochanter separated from femoral head by distinct notch: absent (0), present (1).
99. Greater trochanter joined to femoral head by ridge: present (0), absent (1).
100. Lesser trochanter position: on ventromedial surface of femoral shaft (0), on medial surface of femoral shaft (1).
101. Vertebral centra: amphicoelous (0), platycoelous (1).

APPENDIX 2: CHARACTER STATES

States are denoted as 0 (primitive); and 1, 2, or 3 (derived). ? = state unknown.

	1	1111111112	2222222223	3333333334	4444444445
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890
Gorgonopsid	0000000000	000??00100	0000000000	000000000?	0000000020
Lycosuchus	0000000000	000??00000	0000000000	010000000?	0000000000
Dvinia	0101010010	1110010000	00010?1100	1211101100	0000110000
Procynosuchus	0101010010	1110010000	0001001100	1211101100	0000110000
Galesaurus	0101010011	1110010100	0101101100	1211101100	0000211110
Thrinaxodon	0101010111	1220010100	0101101100	1211101100	0000211110
Cynognathus	0101010111	1220010210	1201211101	1211101110	0001211220
Diademodon	01010101?1	1220010211	1201211201	1211101110	0011211220
Trirachodon	0101010121	1220110211	1201212201	1211101110	0011211220
Pascualgnathus	?101010121	1220110211	1201212201	1211101110	0?11211220
Scalenodon angustifrons	0101010121	1220011211	1201212201	1211101110	0111211220
"*Scalenodon*" *hirschoni*	010101?121	122011??11	?2?121??01	1?111011?0	0??1211220
Luangwa	?101010121	1220?1?211	1201212201	121110111?	0111211220
Massetognathus	1101010121	1220211211	0201212201	1211101110	0111211220
Gomphodontosuchus	?10101?121	122001??1?	?20121??01	1?111?11?0	0??1211220
Exaeretodon	?101011121	122011?210	12?1212201	1211101110	0?11211220
Tritylodontidae	1111101121	1220211211	0211112211	1211111110	0210211221
Lumkuia	0101011120	1220110100	0101201101	1211101100	0011211220
Probainognathus	1101011121	1221110100	0111201101	1211101100	0111211220
Ecteninion	?101011121	1220110?00	0111201101	1211101100	0?11211220
Probelesodon	1101011121	1221210100	0111201101	1211101101	1111211220
Aleodon	1101011121	1222210?00	011120??01	1?11101102	1??1211220
Chiniquodon	?101011121	1222210100	0111201101	1211101102	1?11211220
Pachygenelus	1111101120	1222210000	0011001101	1211111102	0210211221
Morganucodon	0111101121	1222210000	001?002211	?111111100	0210211221

APPENDIX 3: SYNAPOMORPHIES OF PRINCIPAL TAXA OF CYNODONTIA

Numbers refer to characters in Appendix 1. Numbers in parentheses refer to equivocal synapomorphies under the Delayed Transformation (DELTRAN) option of PAUP.

Cynodontia

2. Nasal–lacrimal contact.
4. Postfrontal absent.
6. Prefrontal–postorbital contact.
9. Ectopterygoid does not contact maxilla.
11. Palatal exposure of maxilla behind canine greater than 20% distance from canine to posterior end of palatine.
12. Secondary palatal plate on maxilla.
13. Secondary palatal plate on palatine.
16. Teeth on pterygoid flange absent.
24. Tabular extends around posttemporal foramen.
27. Groove on prootic extending from pterygoparoccipital foramen to trigeminal foramen.
28. Trigeminal nerve exit via foramen between prootic and epipterygoid.
31. Posteroventral process on quadrate in posterior notch of squamosal.

(32). Ascending process of epipterygoid greatly expanded.

33. Epipterygoid–prootic overlap.
34. Lateral flange of prootic.
35. Epipterygoid–frontal contact.
37. Double occipital condyles.
38. Stapedial foramen with dorsoventral orientation.
45. Dentary masseteric fossa present high on coronoid region.

APPENDIX 2: EXTENDED

				1	1
5555555556	6666666667	7777777778	8888888889	9999999990	0
1234567890	1234567890	1234567890	1234567890	1234567890	1
0000000000	000?0?????	??000?000?	0000000000	0000000000	0
0000000000	000?0?????	??000?000?	0000000000	0120000000	0
0100100011	122110????	??210?000?	000?0??0??	???1001000	?
0100100011	010?00????	??010?000?	0001000000	0011001?00	0
0211100011	000?00????	??0?0?0000	0101000000	0011102?00	0
0211100011	010?00????	??010?0000	0101000000	0011102000	0
1311000001	000?00????	??010?0000	?111100000	0121102?00	0
1311?000?1	0221100100	00110?0000	111110?000	0121112000	0
1311100001	0221100??0	00210?1100	1111100000	012???????	0
1311?000?1	0210010100	001?101200	2111110?00	0??1112000	0
1311000001	1221220000	0011101200	21????????	???1??2???	?
1322111?11	0221221010	1011101201	2?????????	?????????0	?
13110000?1	1221221010	1011101201	2101110000	0??2112000	0
1311201111	1222221000	1010101201	2101110100	012211200?	0
1311101111	0212021011	1110111201	2?????????	?????????0	?
1321110111	0212021111	1110111211	2001110100	1122012000	0
1322112?1	0222121?10	1011??1211	2001110111	1122212111	1
1311100011	000?00????	??010?0000	10011?010?	??????????	0
1311100011	010?00????	??010?0100	1001110???	0??211?000	0
1311100001	0?0?00????	??0?0?0000	??0???????	??????????	?
1311100?1	000?00????	??010?0000	?001110100	012211?000	0
1311100?1	021?00????	??110?0000	1?0?????0?	??????????	?
1311100?1	021?00????	??110?0000	??01110100	???211?000	0
1322111111	110?00????	??010?0210	0001111110	1??2212101	1
1310100111	110?00????	??010?0100	1001111111	1122212111	1

46. Dentary overlap of surangular long.
52. Reflected lamina of angular spoon-shaped plate.
55. Incisor cutting margins smoothly ridged.
59. Canine serrations absent.
60. Postcanines with two or more cusps in line.
74. Lower anterior cingulum or cusp present.
94. Length anterior process of ilium 1.0–1.5 times diameter of acetabulum.
97. Length of pubis between 1.5 and 1.0 times acetabular diameter.

Epicynodontia

10. Interpterygoidal vacuity between pterygoid flanges absent in adult.
18. Zygomatic arch moderately deep.
22. Groove for external auditory meatus moderately deep.
25. Descending flange of squamosal lateral to quadratojugal present.
45. Masseteric fossa extends to lower border of dentary.
47. Coronoid process of dentary extends above middle of orbit.
48. Dentary–surangular dorsal contact midway between postorbital bar and jaw joint.
49. Height of postdentary rod about one half the length of the laterally exposed portion of the rod (distance between base of reflected lamina and jaw joint).
52. Reflected lamina of angular hook-shaped, with depth greater than one half its length.
53. Four upper incisors.

54. Three lower incisors.
82. Expanded plates on ribs.
95. Length of posterior process of ilium greater than diameter of acetabulum.
97. Length of pubis less than diameter of acetabulum.

Eucynodontia

25. Descending flange of squamosal lateral to quadratojugal contacts surangular.
30. Quadrate ramus of pterygoid absent.
44. Dentary symphysis fused.
48. Dentary–surangular dorsal contact closer to jaw joint that to postorbital bar.
49. Height of postdentary rod less than one half the length of the laterally exposed portion of the rod.
51. Reflected lamina of angular less than one half the distance from angle of the dentary to jaw joint.
52. Reflected lamina of angular hook-shaped, with depth less than one half its length.
81. Postcanine replacement pattern of widely spaced waves (three or more teeth per wave).
85. Acromion process on scapula.
92. Manual digit III with three phalanges.
93. Manual digit IV with three phalanges.

Probainognathia

7. Parietal foramen absent.
(9). Ectopterygoid absent.
15. Rear of secondary palate lies below anterior border of orbit.
(43). V-shaped notch separates lambdoidal crest from zygoma.
82. Expanded plates on ribs absent.
88. Procoracoid barely present in or absent from glenoid.

Probainognathia Minus *Lumkuia*

23. Frontal contacts palatine in orbital wall.

Probainognathia Minus *Lumkuia, Ectininion*

(1). Premaxillae form posterior border of incisive foramina.
14. Secondary palate about equal in length to tooth row.
(42). Fenestra rotunda partially separated from jugular foramen by finger like projection.
(86). Scapula constricted below acromion process.
(94). Anterior process of ilium anterior to acetabulum greater than 1.5 times acetabular diameter.
(96). Dorsal profile of ilium flat to concave.

Probainognathus, Pachygenelus, and *Morganucodon*

62. Narrow postcanine lingual cingulum.
78. Axis of posterior part of maxillary tooth row directed toward center of temporal fossa.

Pachygenelus and *Morganucodon*.

3. Prefrontal absent.
5. Postorbital absent.
6. Prefrontal–postorbital contact absent.
(14). Secondary palate longer than tooth-row.
(15). Secondary palate extends posterior to anterior border of orbit.
18. Zygomatic arch slender.
22. Squamosal groove for external auditory meatus shallow.
25. Descending flange of squamosal lateral to quadratojugal absent.
36. Separate foramina in petrosal for vestibular and cochlear nerves.
42. Fenestra rotunda completely separated from jugular foramen.
44. Dentary symphysis not fused.
50. Coronoid mediolaterally thickened.
58. Lower canine reduced in size.
61. Upper postcanines with buccal cingulum.

87. Scapula elongated between acromion and glenoid.
(89). Procoracoid contact with scapula equal to or less than coracoid contact.
91. Ulnar olecranon process present.
95. Posterior process on ilium less than one half diameter of acetabulum.
98. Greater trochanter separated from femoral head by deep notch.
100. Lesser trochanter on medial surface of femoral shaft.
101. Vertebral centra platycoelous.

Chiniquodontidae

(15). Secondary palate extends posterior to anterior border of orbit.
41. Posterolateral end of maxilla forms right angle ventral to jugal contact.

Cynognathia

18. Zygomatic arch very deep.
19. Zygomatic arch extends above middle of orbit.
21. Suborbital process on jugal.
22. Groove for external auditory meatus very deep.
26. Basisphenoid internal carotid foramina absent.
39. Greatest width of zygomatic arches at posterior end of arch.
59. Canine serrations present.
83. Lumbar costal plates with ridge overlapping preceding rib.

Gomphodontia

20. Depth of jugal in zygomatic arch greater than twice that of exposed part of squamosal.
28. Trigeminal nerve exit via two foramina.
(43). V-shaped notch separates lambdoidal crest from zygoma.
62. Upper postcanine internal cingulum lingually expanded.
63. Upper postcanines with three cusps in transverse row.
73. Lower postcanines with two cusps in transverse row.
(96). Dorsal profile of ilium flat to concave.

Traversodonts (Incl. Tritylodontidae)

75. Posterior basin on lower postcanines.
(78). Axis of posterior part of maxillary tooth row directed toward medial rim of subtemporal fossa.
81. Adult postcanine replacement pattern consists of single wave.
86. Scapula constricted below acromion process.

"*Scalenodon*" *hirschoni* + Tritylodontidae.

(53). Three upper incisors.
54. Two lower incisors.
(56). Some or all incisors enlarged.

Gomphodontosuchus + *Exaeretodon*

63. Two cusps in transverse row on upper postcanines.
65. Central cusp of upper transverse row absent.
70. High anterior transverse ridge on upper postcanines.
72. Transverse axis of postcanine crowns strongly oblique to midline axis.
(74). Lower anterior cingulum or cusp absent.
76. Widest lower cusp in transverse row buccal.